On the visual tracking of continuous and apparent motion stimuli: saccadic and smooth pursuit tracking components and their relationship to motion sensitivity

Sabrina Maeder

BSc (Hons) University of Tasmania

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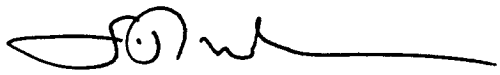

Sabrina Maeder

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Abstract

The present thesis uses continuous and apparent motion stimuli to investigate saccadic and smooth pursuit visual tracking eye movements and their relationship to visual motion processing. The aims were as follows: first, to examine the limits and coordination of saccadic and smooth pursuit components of visual tracking in response to apparent motion stimuli in comparison with traditional continuous motion over a wide range of target velocities. A second aim was to investigate the relationship between visual tracking and visual motion perception. In the present thesis visual tracking of continuous motion was compared with two different types of apparent motion stimuli, which systematically fractured the motion stimulus by manipulating the spatial and temporal components of the target signal in order to investigate their effect on smooth pursuit and saccadic eye movements. In addition, evidence for shared inputs to motion perception and smooth pursuit eye movements was investigated by comparing their performance in response to both continuous and apparent motion stimuli under very similar experimental conditions. Three experiments were conducted. Experiment 1 investigated visual tracking of a single dot in continuous motion at nine target speeds (ranging from 2.5 – 40.0 deg/s) in males and females of different age groups (ranging from 18-39 years). This experiment provided a baseline for subsequent studies of apparent motion generated visual tracking and also evaluated different methodologies used to describe and quantify the saccadic component of visual tracking. The findings of Experiment 1 showed no significant age and gender differences. It revealed a significant saccadic contribution to visual tracking at all target velocities and identified the measure of the ratio of distance covered by saccadic versus pursuit eye movements (Ross et al.,

1999) as the preferred measure of saccadic tracking. Experiment 2 used two kinds of apparent motion stimuli to elicit visual tracking, an intermittently presented stationary target (*jumping-dot motion)* and an intermittently presented moving target (*slashed motion).* These were presented at three stimulus durations (20, 60, 100ms) and five spatial separations (0.5, 1.0, 2.0, 4.0, 5.0 deg) and compared with the tracking of a continuously moving target at nine target velocities (ranging from 2.5-35.0 deg/s). This study aimed to investigate the interplay of saccadic and smooth pursuit eye movements during visual tracking as a function of stimulus velocity and the spatio-temporal stimulus parameters that result in the two kinds of eye movements. The results demonstrated that single-mode pursuit gain elicited by continuous motion decreased linearly with increasing target speed, in conjunction with a parallel increase in saccadic tracking. In contrast, single-mode pursuit gain of apparent motion displayed an inverted U-shape function with increasing target velocity and the optimal velocity resulting in peak smooth pursuit gain depended on the spatial separation, stimulus duration and type of apparent motion stimulus. At target velocities below optimal velocity for peak smooth pursuit gain, a large number of small saccadic eye movements were generated, and at target speeds above the optimum, a small number of larger, faster, and temporally longer saccades were produced. In order to further investigate the lower limits of the saccadic and smooth pursuit components in visual tracking a final experiment was conducted, which extended the velocity range downwards to 1.0-24.0 deg/s for the visual tracking of continuous and apparent motion stimuli at 2.0 deg spatial separation and 60ms stimulus duration. This was compared with motion sensitivity in order to investigate a link between motion perception and smooth pursuit eye movements. The results of Experiment 3 replicated the inverted U-shaped (band-pass) function

with increasing target velocity for single-mode pursuit gain elicited by apparent motion stimuli and revealed a similar band-pass function for single-mode pursuit gain in response to continuous motion, which peaked at 2.0 deg/s target velocity. These findings demonstrated that smooth pursuit eye movements reach peak single-mode gain at an optimal velocity that depends on the spatio-temporal characteristics of the target stimulus. Single-mode pursuit gain decreases when target velocity is above or below a given optimal velocity. The contribution of saccadic eye movements increases when single-mode pursuit gain decreases, but the nature of this contribution is different above and below optimal velocity for peak smooth pursuit gain. When target speed decreases below a given optimal target velocity for smooth pursuit eye movements a large number of smaller, slower, and briefer saccades are generated. In contrast, a smaller number of saccades of larger amplitude, peak velocity and duration are produced when target speed increases beyond optimal pursuit velocity. This demonstrates a more complex and extensive contribution of saccades to visual tracking rather than the one-dimensional process of an increase in saccade frequency and amplitude with increasing target velocity that has traditionally been suggested in the literature. The findings are more consistent with recent models of the coordination of saccadic and pursuit eye movements in visual tracking proposed by Krauzlis (2005) or Orban de Xifry and Lefèvre (2007), which suggest a much closer link between saccadic and smooth pursuit eye movements that are based on shared visual processing and shared target selection. In addition, the profile of the functions for motion sensitivity and single-mode pursuit gain for continuous and apparent motion stimuli displayed many similarities, which provides strong support for the view that motion perception and smooth pursuit have shared inputs. It is concluded that the current findings

demonstrate the conceptual and methodological usefulness of employing continuous and apparent motion stimuli in investigating visual tracking because continuous, slashed, and jumping-dot motion stimuli can be seen to exist on a continuum that allows fracturing the motion signal in a systematic way, providing graded levels of visual motion energy. Thus, these stimuli have great potential to further investigate shared inputs into saccadic and smooth pursuit eye movements and its underlying mechanisms. In addition, they have a particular application to the study of disordered visual tracking, particularly in schizophrenia, in which the origin of the deficit has not yet been identified in relation to saccades, smooth pursuit, or motion perception.

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Table of Contents

Electronic Appendices on CD

List of Tables

List of Figures

Chapter 1

Overview of the Thesis

Since Dodge (1903) first described and classified eye movements, smooth pursuit and saccadic eye movements have been studied extensively. The study of eye movements is a source of valuable information for scientists from different fields, because they are the least complex of motor actions and are therefore easier to interpret than movements of the axial or limb musculature. Many abnormalities of eye movements are distinctive and can indicate a specific pathophysiology or underlying disturbances in neurological sites or processes (Leigh & Zee, 1999). When the link between eye movements and schizophrenia, which had been described by Diefendorf and Dodge (1908), was re-discovered by Holzman (Holzman, Proctor, & Hughes, 1973; Holzman et al., 1974), the study of eye movements in general, and visual tracking in particular, started to receive even more attention, and this interest has remained until today.

Although disordered visual tracking is present in other clinical and neurological conditions, the visual tracking deficit in patients with schizophrenia has received particular attention for several reasons. Unlike in other psychiatric disorders, the visual tracking deficits in schizophrenia are more severe (e.g., Lencer, Trillenberg et al., 2004) and are present even when patients are in remission (Iacono & Koenig, 1983; Iacono, Peloquin, Lumry, Valentine, & Tuason, 1982). The visual tracking deficits are not only present in the patients with schizophrenia, but about 40% of their unaffected first-degree relatives (Clementz, Reid, McDowell, & Cadenhead, 1995;

Holzman et al., 1974; R. G. Ross et al., 2002) also have abnormal visual tracking (but see Boudet et al., 2005), unlike relatives of individuals with affective disorders (Levy et al., 1983). Similarly, individuals at risk of developing schizophrenia (Nieman et al., 2007) and people with schizotypal personality disorder (Siever et al., 1990) or high in schizotypal traits (Kelley & Bakan, 1999; Lenzenweger & O'Driscoll, 2006) also show eye movement abnormalities and there is evidence from twin studies that eye tracking is a heritable trait (Katsanis, Taylor, Iacono, & Hammer, 2000). The visual tracking deficit it is one of the most consistently found biological changes associated with schizophrenia (Hong, Avila, & Thaker, 2003). This has led to the idea that these abnormal eye movements may constitute an endophenotype or biological trait marker for schizophrenia (Calkins, Iacono, & Ones, 2008; Clementz & Sweeney, 1990; K.-H. Lee & Williams, 2000; R. G. Ross et al., 2002), reflecting an underlying genetic vulnerability and neuropathology in schizophrenia (K.-H. Lee & Williams, 2000). Identifying the structures and mechanisms underlying the tracking dysfunction may therefore shed light on the neuropathology of schizophrenia. In addition, because there is no established cause and no defining characteristic for schizophrenia, it has been considered that the visual tracking deficit may be the one characteristic that is common to all individuals with schizophrenia. The eye movement deficits in schizophrenia have been related to illness subtypes (e.g., K. H. Lee, Williams, Loughland, Davidson, & Gordon, 2001) to assist with classification for this heterogeneous illness. Studies have generally reported more severe tracking abnormalities for negative than for positive symptoms (D. E. Ross et al., 1997; Slaghuis, Bowling, & French, 2005), although this effect is not consistently found (Nkam et al., 2001). Recent models of schizophrenia suggest that there may be 11 or

more valid syndromes in schizophrenia (Bruno, 2005), and studies using visual tracking may contribute to validate such efforts.

It is currently not clear what causes the visual tracking deficit in schizophrenia and the possibilities include defective saccadic or smooth pursuit eye movement systems, or motion perception deficits. However, the relationships between saccadic and smooth pursuit eye movements, and between motion perception and eye movements in observers with normal tracking ability are not yet fully understood. It is unlikely that the origin of the tracking deficit in schizophrenia will be resolved without first properly understanding visual tracking in normal observers. The current thesis aims to investigate the interplay between saccadic and smooth pursuit eye movements and the relationship between motion perception and visual tracking in normal observers. Only when these relationships are well understood can the visual tracking deficit in schizophrenia be properly investigated.

For many years, when visual tracking was investigated, the whole tracking response was analysed, until Bahill, Iandolo, and Troost (1980) highlighted the importance of separating the smooth pursuit and saccadic components. Despite this, the saccadic contribution to visual tracking has been somewhat neglected with smooth pursuit eye movements receiving most of the attention. In recent years the interest in saccadic tracking has increased and the question has been raised as to how the two types of eye movements work together when visually tracking a target. There is now some evidence that the two kinds of eye movements may share some underlying mechanisms and processes or may even be two different outcomes of a single system (Krauzlis, 2004, 2005; Orban de Xifry & Lefèvre, 2007). Also, the link between

motion perception and particularly smooth pursuit eye movements has repeatedly been made in recent years, especially when it was suggested that disordered visual tracking in schizophrenia may be due to underlying motion perception deficits. There is now evidence that motion perception and smooth pursuit eye movements are, in the very least, very tightly linked (Keller & Heinen, 1991), and may even have shared inputs, although this proposed link is not yet very well understood or generally accepted. Similarly, we do not yet understand the processes underlying the collaboration between saccadic and smooth pursuit eye movements during visual tracking, and the current thesis aims to examine these areas of enquiry.

Chapter 1 provides a brief overview of the thesis, Chapter 2 introduces eye movements and their general anatomy and classifications. The focus of the chapter is on saccadic and smooth pursuit eye movements, as they together make up the visual tracking response. The chapter describes in detail the parameters of saccades and smooth pursuit, as well as theoretical models and significant topics relating to these two types of eye movements. Chapter 3 describes the main neuro-anatomical structures that are part of the saccadic and smooth pursuit systems and outlines the neurological pathways traditionally associated with the generation and control of each type of eye movement. The chapter then discusses the recent notion of shared inputs into saccadic and smooth pursuit eye movements, and the possibility that the two kinds of eye movements may reflect two different motor outcomes of a single underlying eye movement system.

The focus of Chapter 4 is on visual tracking. The saccadic and smooth pursuit contributions to visual tracking are first described individually, as well as the effects

they have on each other. The chapter then discusses what little is currently known about the coordination of the two eye movements during visual tracking, as an important aim of this thesis is to further investigate this area. Then, apparent motion is introduced and how this type of motion has been used in the study of visual tracking, because the current thesis uses different types of apparent motion to investigate smooth pursuit and saccadic tracking and motion perception.

Chapter 5 is concerned with visual perception of motion. It provides a general overview of the main concepts and parameters of motion perception, as well as a more detailed description of motion perception models. The chapter also describes the general neuro-anatomical structures and pathways involved in the perception of motion. The chapter concludes with a discussion of potential shared inputs into motion perception and saccadic and smooth pursuit eye movements and another important aim of this thesis is to further investigate this idea.

The series of experiments are reported in Chapters 6, 7, and 8. Chapter 6 reports and discusses the findings of Experiment 1, which investigates saccadic and smooth pursuit components of visual tracking using continuous motion. It aims to accurately describe and quantify saccadic and smooth pursuit tracking contributions across a wide range of target velocities. In particular, there are inconsistencies in the literature with regard to measures of saccadic frequency, which need to be clarified before further investigating visual tracking. Chapter 7 reports the second experimental study and discusses its findings. This study systematically investigates saccadic and smooth pursuit visual tracking components and their synergy in response to two different types of apparent motion stimuli across a wide range of spatial and temporal

parameters. This includes a jumping-dot (intermittent presentation of stationary targets) and a slashed motion (intermittent presentation of a moving target) paradigm and for the first time visual tracking of these are directly compared with each other, as well as with tracking of continuous motion. The final experiment is reported and discussed in Chapter 8. This study aims to compare performances of visual tracking and motion perception in order to investigate the notion of shared inputs of the two. Motion sensitivity and saccadic and smooth pursuit tracking of continuous and apparent motion stimuli is directly compared under similar experimental conditions. The thesis concludes with a general discussion of all empirical findings in the context of the previous literature and the aims of the thesis (Chapter 9).

Chapter 2

Saccadic and smooth pursuit eye movements

The movements of the eyes

Introduction

The human eyes are constantly moving, over 100,000 times per day (Kleiser, Seitz, & Krekelberg, 2004), and yet, we are usually not aware of any movement but see the world as stable. Indeed, it is often argued that it is because of constant eye movements that the world can appear stable (R. H. S. Carpenter, 1988, 1991; Gregory, 1958; J. Ross & Ma-Wyatt, 2003; Walls, 1962). Vision is most detailed in the fovea and the eyes move continually with the main aim of bringing or retaining objects in this small high-acuity area (Leigh & Zee, 1999; Wirtschafter & Weingarden, 1988). However, even when the eyes appear still, and fixated on an object, they constantly make miniature movements of a few minutes of arc (R. H. S. Carpenter, 1988). Without these eye movements the visual world would fade away or even disappear (Gregory, 1958; Walls, 1962), because they serve to overcome the effects of local adaptation. These fixational movements consist of slow, smooth movements (Kowler, 1990, 1991; Leigh & Zee, 1999; Sperling, 1990), partly to compensate for unwanted perturbations of the head (Leigh & Zee, 1999), interspersed with microsaccades (R. H. S. Carpenter, 1988), as well as saccadic intrusions and their corrections (Abadi & Gowen, 2004). It has been suggested that these micro-movements are merely a consequence of instability in the oculomotor system (Fender & Nye, 1961), to which the visual system then adjusted in turn (R. H. S. Carpenter, 1988). More recent evidence, however, suggests that they have evolved to adapt to and maximise the visual system and its edge-sensitive visual fields for the

discrimination of fine spatial detail (Rucci, Iovin, Poletti, & Santini, 2007). Apart from these constant miniature movements, there are other common eye movements, such as visual search or exploratory eye movements, including saccades, smooth pursuit and vergence (Hallett, 1986), that used in everyday life. These are not generated randomly, but are very closely linked to cognitive goals and processes (Yarbus, 1967) with a strong attentional component (Hoffman, 1998). They orient, direct, monitor, and guide general locomotion (Wilkie & Wann, 2003) and other everyday activities (Hayhoe & Ballard, 2005; Land, Mennie, & Rusted, 1999), as well as specific tasks, such as reading (see Rayner, 1998) or driving (e.g., Land & Lee, 1994).

There is considerable variation between species in regards to their ocular motility and this has been related to the size of their visual field (R. H. S. Carpenter, 1988, 1991). Humans and other primates have a relatively small visual field and make frequent eye movements to foveate objects, often combined with head movements to maximise visual performance. However, while it makes sense that species whose eyes have a fovea have increased ocular motility, some species (e.g., the owl) solve this problem with increased head movements, while others (e.g., most types of fish) have no fovea but make frequent eye movements (Walls, 1962). Another reason why humans have high ocular motility is that, unlike many other species, the vision of humans and their close relatives is coordinated binocularly, allowing for precisely synchronised movements in the same (conjugate) and even opposite (disjunctive) directions (Walls, 1962). This strongly binocular mechanism, together with the presence and relatively small size of the fovea, are believed to be the main reasons why primates have such

high ocular motility. The present chapter describes and classifies all types of human eye movement, although its focus is on saccadic and smooth pursuit eye movements.

Classification of eye movements

There are many ways to classify the various types of eye movements; one of the first was suggested by Raymond Dodge (1903). He distinguished between five types of eye movements; *type I movements* (saccades), *pursuit movements*, *compensatory movements* (vestibular eye movements), *reactive compensatory movements* (fast-phase of nystagmus), and *vergence eye movements*. Even though the current classification has changed to some degree from these original propositions, Dodge was the first to classify eye movements not solely on the basis of their velocity, but also taking into consideration their stimulus and context. Traditionally, the broadest classification is to distinguish between abrupt (or ballistic) and smooth eye movements, as well as whether both eyes are moving in the same (conjugate) or opposite directions (disjunctive) (Hallett, 1986, see Figure 1). A classification between eye movements is sometimes also made in terms of their purpose (R. H. S. Carpenter, 1988, 1991; Leigh & Zee, 1999), making the distinction between gaze-holding (or gaze-stabilising) and gaze-shifting movements.

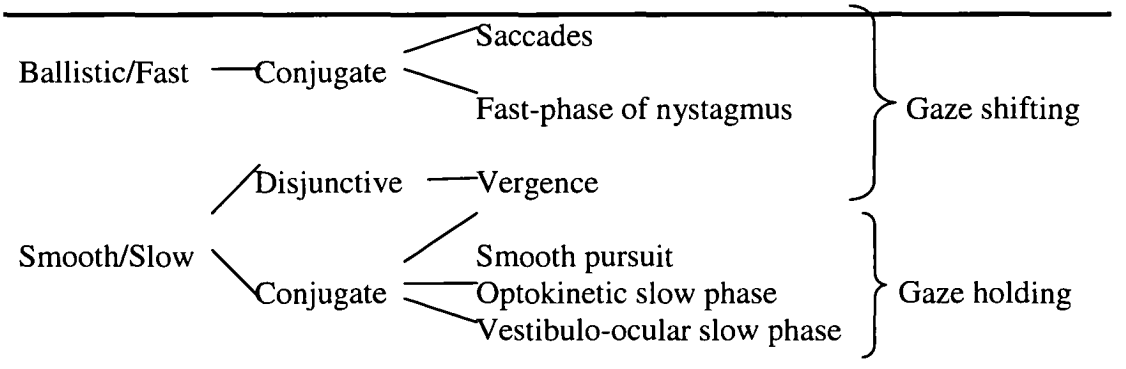

Figure 1. Classification of human eye movements (adapted from (R. H. S. Carpenter, 1988; Hallett, 1986).

However, this classification system is somewhat ambiguous. For example, the optokinetic reflex includes both gaze-holding and gaze-shifting components, and smooth-pursuit could also be classified as gaze-holding (Kowler, 1990). Furthermore, although saccadic and smooth pursuit eye movements are generally conjugate in the plane, they have disjunctive components in depth (e.g., tracking an object in depth).

Abrupt eye movements consist of brief and very fast ballistic movements of the eyes, during which vision is temporarily suppressed. These include saccades and the fast phase of nystagmus. Saccades are short (20-100ms) and fast (200-600 deg/s peak velocity) ballistic movements aimed at foveating an object of interest (Hallett, 1986). On average, humans make 3-4 saccades per second (J. Ross, Morrone, Goldberg, & Burr, 2001). Their size can vary considerably, from a few minutes of arc (i.e., "microsaccades") to 60 degrees of visual angle (R. H. S. Carpenter, 1988). Saccades are generally classed as a voluntary eye movement, although the majority of saccades in everyday life are made automatically and without the conscious awareness of the observer, and novel or threatening stimuli evoke saccades even if observers are instructed not to respond (Hallett, 1986). Furthermore, saccades are a crucial component in many cognitive tasks, such as reading, scanning, and visual search (see Rayner, 1998, for a detailed review of this field). Nystagmus is an oscillation of the eyes that can be either a pendular or a jerk waveform (Dell'Osso, 2002), and is caused by instabilities in slow eye movement systems Jerk nystagmus is a rapid alternation of a smooth (*slow phase*) eye displacement away from a target and a ballistic (*fast phase*) eye movement in the opposite direction in an attempt to refoveate the target (Hallett, 1986). In pendular nystagmus (also called pursuit-system nystagmus) the eye alternates using slow movements, with occasional saccadic corrections (Jacobs &

Dell'Osso, 2004). Rapid alternations of saccadic movements (called saccadic oscillation) also exist, but they are associated with instabilities of the saccadic system (Dell'Osso, 2002) and not included in the definitions of nystagmus. While some individuals can produce nystagmus voluntarily, it is usually an involuntary and prolonged condition, which can be congenital (Harris, 1995) or acquired (e.g., after cerebral lesions, R. H. S. Carpenter, 1988). Nystagmus can sometimes also be transient; associated with disease (e.g., positional vertigo, Fletcher, 1952; von Brevern, Zeise, Neuhauser, Clarke, & Lempert, 2005), substances, such as lithium (Bourgeois, 1991), or nicotine (Pereira, Strupp, Holzleitner, & Brandt, 2001), or by extensive stimulation of the eyes through external stimuli (Pasik, Valciukas, & Pasik, 1973). Saccades and the fast-phase of nystagmus share very similar underlying motor circuits, including muscle activity (Leigh & Zee, 1999), and they are sometimes reported as one type of eye movement (Westheimer, 1989), although the two differ at higher levels of processing (Hallett, 1986), with the fast-phase of nystagmus being less under volitional control (Becker, 1989), and most saccades having significantly more cognitive input (Rayner, 1998). This is consistent with the notion that the fast-phase of the nystagmus reflects a 'normal' reflexive saccade in an attempt to correct the error caused by the nystagmus slow phase (Dell'Osso, 2002).

Smooth eye movements can be either conjugate or disjunctive and are slow movements which can be sustained over much longer durations than fast movements. Smooth eye movements that are conjugate in the plane include the slow phases of the optokinetic and vestibulo-ocular reflexes, the slow phase of nystagmus, and smooth pursuit. The main disjunctive smooth movement is vergence, although other smooth eye movements can include disjunctive components when targets move in depth. The

optokinetic reflex is a combination of a smooth tracking eye movement in one direction, and a 'reset' saccade in the opposite direction (Collewijn, 1991), allowing the observer to track sequential objects in motion (e.g., looking at trees while travelling in a train). In humans, smooth pursuit and the slow phase of optokinetic movements are sometimes believed to be quite similar and to have the same underlying neurology (Hallett, 1986; Kowler, 1990), although others suggest that they are somewhat separate eye movements (Krauzlis, 2004; Lisberger, Morris, & Tychsen, 1987). The vestibulo-ocular reflex is a very common and effective eye movement that stabilises an image on the retina during head movements, by producing smooth eye movements in the opposite direction of the head movements (e.g., it allows one to remain fixated on an object while shaking one's head or nodding). It is this reflex that allows people to see while moving around (D. A. Robinson, 1981) and is found in most animals, as it is the phylogenetically oldest ocular movement (Walls, 1962). This reflex is very accurate, has a short latency (below 15ms) and can be very fast (up to 500 deg/s) (Hallett, 1986).

Smooth pursuit is the smooth and generally voluntary movement of the eyes while tracking an object. Unless tracking an object in depth, in smooth pursuit the eyes move conjugately at velocities up to 100 deg/s (although it becomes less accurate at speeds above 30 deg/s) to keep the object image near the fovea to provide high acuity viewing of the moving target (Pola & Wyatt, 1991). Pursuit eye movements are phylogenetically the most recent oculomotor system, and are only fully available to humans and primates as they have central vision (Eckmiller, 1987; Walls, 1962). It has been suggested that smooth pursuit evolved out of the vestibulo-ocular reflex, prompted by a need for keeping targets in central vision during self-motion (S. A. Miles, 1998). Vergence consists only of disjunctive eye movements, with both eyes

move simultaneously in opposite directions, thereby changing the angle between the visual axes of the two eyes (Judge, 1991). Vergence movements are concerned with the proximal location of objects (Pola, 2002), for example, they occur if a foveated object moves towards or away from the observer. These movements rarely exceed velocities of 10 deg/s and mainly occur to obtain or maintain coordinated binocular vision by facilitating fusion of the retinal image of the two eyes (Hallett, 1986).

The oculomotor system also includes a number of other specific kinds of eye movements, which are sometimes classified separately. For example, glissades (Weber & Daroff, 1972), also called postsaccadic drift (Becker, 1989, 1991), are slow, long-duration eye movements, which correct the position of the eye after an inaccurately executed saccade (Becker, 1989; Dell'Osso, Daroff, & Troost, 1972), usually associated with a fatigued saccadic system (Bahill, Brockenbrough, & Troost, 1981; Bahill & Stark, 1975). They have no latency and are typically of 1.1 deg amplitude (range: 0.2-5.0 deg), 8.0 deg/s velocity (range: 0.5-20.0 deg/s) and 250-500ms duration (Hallett, 1986). Hallett (1986) reported that back-drifting glissades were twice as frequent as forward-drifting glissades, while Becker (1989) reported a prevalence of backward glissades in the adducting eye (the eye moving from temporal to nasal position) and a prevalence of forward glissades in the abducting eye (nasal to temporal direction). There are also many smooth and abrupt movements which are used in social interactions to communicate specific information (e.g., rolling the eyes) (R. H. S. Carpenter, 1988).

Anatomy of the oculomotor system

The remarkably varied and complex movements of the eyes are executed by the synergetic actions of three pairs of extraocular eye muscles, which were first described in detail by Bell (1823). These are the medial and lateral recti, the superior and inferior recti and the superior and inferior obliques (see Figure 2) and they are considered to be some of the fastest-moving muscles in mammals (Spencer & McNeer, 1991). A seventh muscle, the levator papebrae superioris (Gray, Ellis, Berkowitz, & Standrig, 2005) is sometimes included in the classification, although it does not directly move the eyeball, but is responsible for elevating the upper eyelid. The ocular muscles are made up of at least six different types of fibre (Spencer & McNeer, 1991), varying in diameter, composition, position within the muscle, as well as their mechanical and electrical properties (R. H. S. Carpenter, 1988; Peachey, 1971). The four recti have between 20,000-30,000 fibres in each muscle, while the obliques have just under 20,000 fibres each. Usually all three muscle pairs are active simultaneously, enabling the varied types of eye movements across the multiple dimensions of which the human eye is capable. The extraocular muscles are innervated by three main cranial nerves, the oculomotor nerve (III), the trochlear nerve (IV), and the abducens nerve (VI), which receive their signals from brainstem nuclei (M. B. Carpenter, 1971).

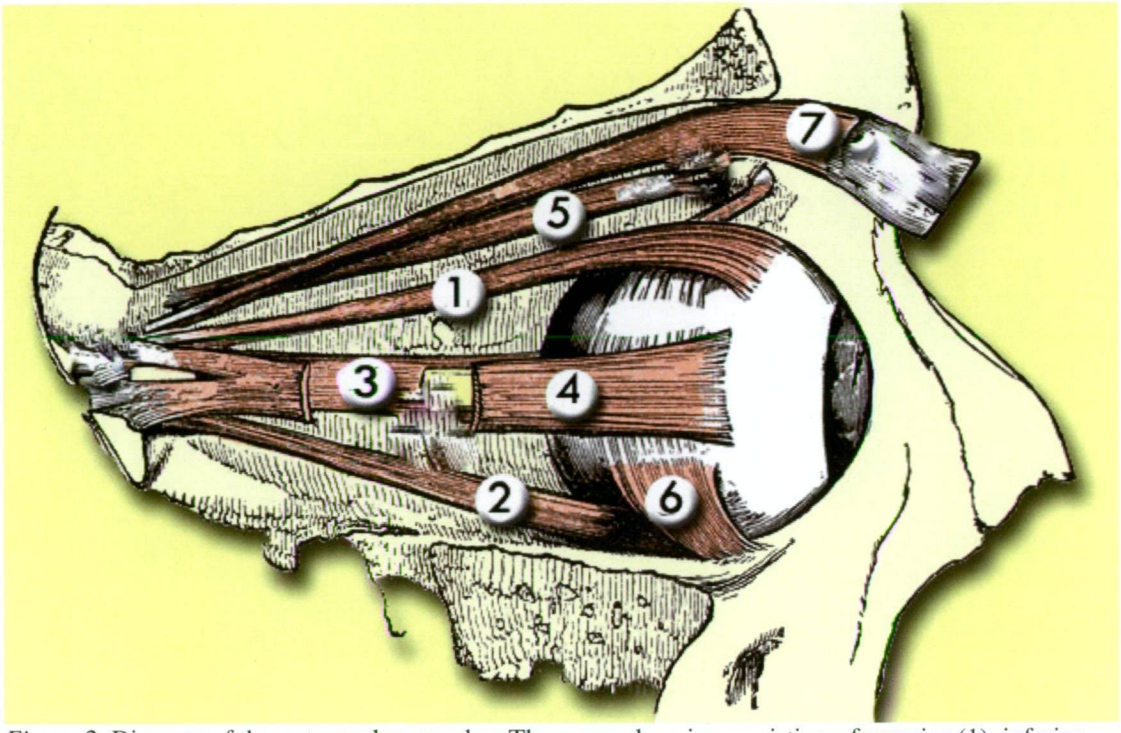

Figure 2. Diagram of the extraocular muscles: Three muscle pairs consisting of superior (1), inferior (2), (3) medial, and (4) lateral rectus muscles and superior (5) and inferior (6) oblique muscles. (7) is the levator palpebrae superioris which moves the eye lid (adapted from Gray et al. 2005, p.692).

Saccadic eye movements

Introduction

The term saccade comes from on the French word 'saccade', which means 'jerk', based on their ballistic and step-like manner, compared with the continuous and fluent smooth eye movements. The main goal of saccades is to foveate objects of interest (Bahill & Troost, 1979). There have been attempts to classify saccades into subcategories by criteria such as whether or not they are goal-directed (Becker, 1989), are voluntary or reflexive (Sharpe, 1998; Walker, Walker, Husain, & Kennard, 2000; Walls, 1962), their accuracy (Bahill & Troost, 1979), latency (Fischer & Boch, 1991), or various other characteristics (Hallett, 1986). However, while there certainly are some differences between different types of saccades, their general profile is sufficiently similar to treat them as one type of eye movement with very similar

underlying mechanisms (Findlay & Walker, 1999; Hallett, 1986) and neurological pathways (Hepp, Henn, Vilis, & Cohen, 1989). The fast phases of nystagmus and optokinetic and vestibulo-ocular reflexes are usually mentioned and discussed separately, but even these eye movements are believed to share their basic neurological pathways (Hallett, 1986).

Saccadic suppression

One feature of saccadic eye movements that was first described by Dodge (1900) was our inability to see our own fast eye movements, indicating that vision must somehow be suppressed or at least reduced during saccadic eye movements. During saccades the image of the world sweeps over the retina and should therefore produce a smeared image or 'greyout' (Campbell & Wurtz, 1978), but instead we see a stable image of the world. This 'saccadic suppression' precedes the saccade by about 40-50ms (R. H. S. Carpenter, 1988; Diamond, Ross, & Morrone, 2000), is maximal at saccade onset and continues until 50ms (Diamond et al., 2000) to 100-120ms (R. H. S. Carpenter, 1988) after saccade completion. Whereas initially vision was believed to be completely 'anaesthetised' (Holt, 1903) later studies indicated that while visual thresholds were clearly elevated, vision was not totally absent during saccades (see Volkmann, 1986, for a historical review). A number of models have been proposed to describe and explain the underlying mechanisms of saccadic suppression (e.g., Breitmeyer, 1984; Matin, Clymer, & Matin, 1972). One explanation that has been proposed is that what is suppressed during saccadic eye movements is motion information (Burr, Morgan, & Morrone, 1999; Diamond et al., 2000; Ilg & Hoffmann, 1993; J. Ross et al., 2001; Sperling, 1990), with specific suppression of magnocellular pathways (Burr, Morrone, & Ross, 1994; Kleiser et al., 2004), while

sparing, or even enhancing, the parvocellular pathways. These are not universally accepted though and other studies have found that some motion perception is possible during saccades (Castet & Masson, 2000; Garcia-Perez & Peli, 2001), and motion processing immediately after a saccade has been found to be more sensitive than before the saccade (Ibbotson, Price, Crowder, Ono, & Mustari, 2007; Reppas, Usrey, & Reid, 2002).

Helmholtz (originally in 1866, see 1963) and later Sperry (1950) and Von Holst and Mittelstädt (1954) were among the first to offer a theoretical explanation of the mechanisms underlying saccadic suppression; what is now generally referred to as 'corollary discharge' theory (see e.g., Campbell & Wurtz, 1978; J. Ross et al., 2001). This theory postulates that saccades are accompanied by a 'corollary discharge' or 'efference copy' of the motor signal, which allows identifying the motion as self-generated and therefore cancels the subsequently perceived image motion. There are many supporters of this view (Burr, 2004; Diamond et al., 2000; P. H. Lee et al., 2007; J. Ross et al., 2001; Tatler & Troscianko, 2002), but alternative explanations of saccadic suppression have also been proposed. These include the view that motion perception is not actually suppressed, but merely masked by either the visual images before and after the saccade (Breitmeyer, 1984; Campbell & Wurtz, 1978; Castet & Masson, 2000; Ciuffreda & Tannen, 1995; Matin et al., 1972), or by the visual motion caused by the eye movement itself (Mackay, 1970). More recently, attempts have been made to identify the neurological site of saccadic suppression, and some preliminary findings indicate that saccadic suppression may take place early in the visual pathway between the retina and the occipital visual cortex (Thilo, Santoro, Walsh, & Blakemore, 2004) in the lateral geniculate nucleus (Burr, 2004; Burr et al.,

1994; Diamond et al., 2000; Reppas et al., 2002). Other have suggested the intermediate layers of the superior colliculus (P. H. Lee et al., 2007) or visual cortical areas, such as MT, MST or V4 (Burr, 2004; Ibbotson et al., 2007; Kleiser et al., 2004; Thiele, Henning, Kubischik, & Hoffmann, 2002; Thilo et al., 2004) as possible sites for saccadic suppression.

The parameters of saccadic eye movements

It has been suggested that saccade need to be very short and efficient because visual input is decreased during saccades (R. H. S. Carpenter, 1988; D. A. Robinson, 1981), and indeed, saccades are all of very short duration, regardless of their function and specific characteristics, and they are also very similar at the motor level. This feature was first quantified by Bahill, Clark, and Stark (1975), who used the astronomy term 'main sequence' to describe the stable linear relationship that exists between saccade duration and magnitude, as well as between peak velocity and magnitude. Since then the main sequence has been widely used to confirm eye movements as saccades (Hallett, 1986), to clinically assess the neurological integrity of the saccadic system (Ciuffreda & Tannen, 1995) and to quantify saccades, although the main sequence relationship between peak velocity and magnitude is somewhat more useful (Bahill et al., 1981). For large saccade amplitudes (above 50-60 deg), the main sequence relationship becomes less linear with large saccades being less stereotyped (Becker, 1989).

Using the main sequence and other saccade characteristics some typical features of saccades have been identified over the years. Generally, saccades are very fast, with peak velocities ranging from 20-600deg/s (Becker, 1989, 1991; Hallett, 1986)

depending on saccade amplitude. Saccade amplitude can vary significantly from a few minutes of arc (microsaccades used during fixation) to 60 deg (e.g., Hallett, 1986) although in real life large saccades (above 15-20deg) are typically accompanied by head movements (Becker, 1989; Findlay & Walker, 1999), and about 85% of naturally occurring saccades are less than 15deg (Bahill et al., 1975). Saccades are usually of very short duration (20-100ms; Hallett, 1986), which means that the eyes have to accelerate and decelerate very fast to cover the distance. It is these sharp acceleration (peak acceleration of 26000-35000deg/s^2, see Becker, 1989) and slightly smaller deceleration phases that result in the very abrupt onset and termination typical of saccades (Hallett, 1986). Although all of these measures are used to describe saccades, peak velocity has emerged as a very popular measure, due to its linear relationship with amplitude and the fact that it is (mathematically) independent of duration, and therefore unaffected by how the beginning and end point of a saccade are defined (Becker, 1989). While these saccade characteristics are fairly stable, they are affected by direction (e.g., saccades to a central position are shorter and faster than those aimed towards the periphery), structure of visual field (e.g., actual versus remembered stimulus), age, instructions, attention, drugs, fatigue and individual variability of observers (Bahill et al., 1981; Becker, 1989, 1991; Hallett, 1986).

Saccades can also be described in terms of their accuracy, which is usually defined in terms of error: the difference between target position and eye position (Becker, 1991). Goal directed saccades can overshoot or (more commonly) undershoot their targets. For example, for horizontal saccades of 20.0-40.0 deg error rates can vary from 10-70%, depending on viewing conditions (Becker, 1989; Ciuffreda & Tannen, 1995).

The errors are generally corrected by a second saccade or a glissade. According to Becker (1989; 1991), if the error was due to a miscalculation in step size, a corrective saccade is triggered, but if the saccade error was due to an error in saccade execution (including a mismatch of the two eyes) postsaccadic drift or glissades are used for correction. Corrective saccades to large errors (2.0-4.0 deg) have a reduced latency (110-150ms), while corrective saccades to small errors (below 1 deg) have normal latencies (180-220ms) (Becker, 1991). This reduced latency for corrective saccades in response to large errors may indicate that these corrective saccades are already planned during the execution of the main saccade (Becker, 1991; Kowler, 1990) or that for large errors the time required to decide whether or not to trigger a saccade is shorter.

Another typical feature of saccades is their relatively long reaction time or latency, which can range from 180 to 220ms (Hallett, 1986; Becker, 1991), although latencies as short as 90-120ms have been reported. These were called 'express saccades' by Fischer and colleagues (Fischer, 1986; Fischer & Boch, 1983; Fischer & Ramsperger, 1984), who postulated that saccade latencies follow a bimodal distribution with peaks at around 100ms (express saccades) and 150ms (fast regular saccades) and sometimes even a third peak around 200-230ms (slow regular saccades). However, these variations in saccade latency depend strongly on the stimulus and the viewing conditions, such as luminance, target amplitude, predictability, stimulus direction, age, handedness, but particularly attention (Becker, 1989; Ciuffreda & Tannen, 1995; Fischer & Weber, 1993; Hallett, 1986; Kowler, 1990), and express saccades are usually associated with highly predictable targets and well practiced subjects (Becker, 1991). Even with its high variability, what is remarkable about saccade latency is how

long its duration is, usually longer than the duration of the actual saccade itself. This long delay in saccade production, which is sometimes called 'saccadic procrastination' (R. H. S. Carpenter, 1988) is puzzling in the visual system, because it is so efficient in many other regards. Becker (1989; 1991) labelled one part of the saccade latency as the 'decision-making time', which accounts for the high variability in saccade latencies and is the component that is affected by the previously mentioned modulating factors. There are also some very constant and known components (ca. 130ms) within the latency (Lisberger, Fuchs, King, & Evinger, 1975), which are fairly stable across individuals. This includes the *afferent delay* (40-60ms) of the signal reaching the cortical visual areas where decision making takes place, the *efferent delay* (20-35ms) of the motor signal of superior colliculus and related areas to reach the muscles, as well as a less well defined '*computational*' delay (35-70ms) required to access and use the computations made during the decision making stage (Becker, 1989; 1991; Ciuffreda & Tannen, 1995). This is consistent with findings that reflexive saccades have shorter latencies compared with voluntary saccades (Walker et al., 2000) and the fact that express saccades occur under conditions that reduce decision times (e.g., highly predictive saccades). One possible explanation for the long saccade latency (described by Kowler, 1990) is that at some stage a saccade becomes irrevocable and will be executed without further feedback, and the visual system delays this point as much as possible to increase saccade accuracy. Another explanation (described by R. H. S. Carpenter, 1988) suggests that because vision is suppressed during saccades, the visual system may delay saccade execution in order to limit the time without visual input (Harwood, Madelain, Krauzlis, & Wallman, 2008). The different available explanations for what processing takes place during the

extensive saccade latency reflect different conceptualisations of the nature of saccade programming and the mechanisms involved.

Models of the saccadic system

Young and Stark (1963) formulated the first model of the saccadic system, conceptualising it as a sampled-data control system, based partly on findings by Westheimer (1954). In this simple mathematical model, information about the position of the current and desired eye position is obtained (in retinal position coordinates) and a saccade is then programmed, initiated and executed without feedback, while the sampling mechanism is refractory for about 200ms. Upon completion of the saccade, a new sample is taken and if required, the process is repeated based on the new information. This model conceptualised saccades as pre-programmed, ballistic movements, executed without any visual feedback, as the very brief duration of saccades was believed to be too short to allow their trajectory to be guided by visual feedback.

Robinson radically changed previous conceptualisations of the saccadic system by proposing a model that included an internal feedback loop (D. A. Robinson, 1973, 1975, 1981). In this model, a local feedback loop compares the current eye position (based on an efference copy) with the desired position, resulting in a 'motor error', which in turn drives the motor signal for saccades, until the motor error reaches zero. Also, rather than coding eye position in retinal coordinates, the model proposed instead that position was computed in relation to the head in space. Subsequent research provided strong support for the local feedback component of the saccadic eye movement system (Becker & Jürgens, 1979; Hallett & Lightstone, 1976; Mays &

Sparks, 1980a). Slightly modified or extended versions of Robinson's original model have since been proposed (e.g., Fuchs, Kaneko, & Scudder, 1985; McKenzie & Lisberger, 1986; Van Ginsbergen, Robinson, & Gielen, 1981). In particular, while Robinson's original model proposed serial processing; subsequent models have suggested parallel processing (Becker & Jürgens, 1979; Findlay & Walker, 1999). This reflects the view that many of the mechanisms involved in saccade programming occur simultaneously, and this is now the generally accepted view. Furthermore, while Robinson's original model proposed that eye *position* was the basic criterion for feedback comparisons, others have suggested that the feedback loop compares different parameters (Abrams, Dobkins, & Helfrich, 1992), such as eye *displacement* (e.g., Becker, 1989; 1991) or eye *velocity* (Fuchs et al., 1985; Scudder, 1988). The proposition that target position is encoded head-centric rather than retinal has received some support (Mays & Sparks, 1980b; Wirtschafter & Weingarden, 1988), but it is not universally accepted (see Findlay & Walker, 1999). Another area of ongoing contention is the specific location and nature of the pathways involved in the feedback loop. For example, some current models propose that the superior colliculus does not form part of the feedback circuitry, which is believed to be in the brainstem (Scudder, 1988; Van Ginsbergen & Van Opstal, 1989). Others propose that the feedback loop includes the superior colliculus (Guitton, 1991), and the cerebellum (Quaia, Lefèvre, & Optican, 1999). However, all of these more recent models are variations on the original Robinson model, in that all the models conceptualise saccades as being produced by local error feedback (Keller, 1991), and they vary only in terms of what stimulus is compared for the error feedback, and what neural structures are involved in the feedback circuitry.

A very important paradigm in the development and extension of the feedback-based model of the saccadic system was the double-step paradigm, which was devised by Becker and Jürgens (1979). In this paradigm, two targets are presented in quick succession and disappear before the onset of the first saccade. Such studies have shown that programming for the second saccade could start before the observer has initiated the first saccade, lending support to the idea that saccade programming is processed in a parallel, rather than a serial manner. They also showed that new information about the visual target and the eye position are continuously available and can influence a saccade until 80-100ms before it is triggered. Hence, while saccades themselves are discontinuous or ballistic in nature, in that they cannot be modified by new information once they are triggered, the saccadic system itself is not ballistic but continuously receives and considers new information, which influences decisions about saccades. Even if it may be too late to use this information for the current saccade, it can be used to start preparing a subsequent saccade (Becker, 1989; Becker & Jürgens, 1979).

Another crucial component that contributed to the development of Robinson's and subsequent models of the saccadic system were neurophysiological advances and subsequent collaboration of different research fields (Van Ginsbergen & Van Opstal, 1989). In particular, findings concerning the firing patterns of single neurons in animals responding to various stimuli uncovered some of the processes involved in saccade generation at the cell level (see D. A. Robinson, 1981, for a review). It is now generally accepted that saccades are generated in a pulse-step manner and the processes involved have been described in detail (Becker, 1989, 1991; Ciuffreda & Tannen, 1995; Fuchs et al., 1985; Guitton, 1991; Hepp et al., 1989; Keller, 1991;

Pola, 2002; D. A. Robinson, 1981; Scudder, 1988; Van Ginsbergen et al., 1981; Van Ginsbergen & Van Opstal, 1989). There are excitatory and inhibitory burst neurons in both the superior colliculus (Wurtz, 1996) and brainstem nuclei (Hepp et al., 1989). Excitatory burst neurons in the brainstem generate an intense signal resulting in the pulse required to produce the high-velocity movement in the direction of the saccades. Inhibitory burst neurons inhibit the motoneurons in the direction opposite to the saccade. Burst neurons are inactive during fixation or smooth movements and their firing pattern is very highly correlated (above 0.9) with saccade characteristics: burst *duration* with saccade duration, peak firing *rate* with peak saccade velocity and number of firing spikes with saccade size (Fuchs et al., 1985). Tonic neurons, on the other hand, show a regular, tonic firing rate, aimed at holding the eye in a position. The role of tonic neurons in saccadic eye movements is to produce the step signal necessary to keep the eye in the new position after completion of the pulse. Both signals are integrated to create the pulse-step command generating the saccade (Ciuffreda & Tannen, 1995). Another important class of neurons are omnipause or pause neurons, which inhibit both excitatory and inhibitory burst neurons, and they fire continuously during fixation and smooth movements but are inactive during saccades (Hepp et al., 1989; Wurtz, 1996).

Cognitive factors in saccadic eye movements

Cognitive factors have also been shown to play an important role in saccadic eye movements (see S. B. Hutton, 2008, for a review). In particular, the role of attention in the generation of saccades has been thoroughly investigated (see Hoffman, 1998) particularly during reading (Rayner, 1992). Available evidence generally supports the view that saccades to a new location are preceded by a shift of visual attention to the

same location (Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshler, & Blaser, 1995), and there is extensive overlap in the underlying neurology of attentional and saccadic tasks (Corbetta et al., 1998). However, there are opposing views; for example, Remington (1980) found that some saccades were not preceded by attentional shifts and suggested that attention is linked to visual events, rather than oculomotor events, and Klein (1980) found a dissociation of attention and saccadic eye movements. Nevertheless, the current view is that attention and eye movements are partially interdependent in that attention can be shifted independently of the eyes, but eye movements require visual attention (Hoffman, 1998). With saccadic eye movements in particular, it is thought that the attentional processes involved in saccade programming include attentional disengagement from the current eye location (Posner, 1995) and an attentional shift to the new location (Becker, 1989). This is consistent with the significantly decreased latencies associated with cued saccades, as the attentional shifts are triggered by the cues therefore saving cognitive decision making time of saccade programming (Becker, 1989; Hoffman, 1998).

Other cognitive factors affecting saccade generation include expectation and prediction (Pavel, 1990). If targets are predictable observers will use prediction to reduce saccade latency (Ciuffreda & Tannen, 1995). Express saccades (Fischer, 1986; Fischer & Boch, 1983; Fischer & Ramsperger, 1984) only occur to highly predicable or even cued targets (Becker, 1991), and saccades can even be made before target appearance in anticipation of the target (Ciuffreda & Tannen, 1995). Prediction reduces the decision-making time (Becker, 1991; Pavel, 1990), although it typically comes at the price of accuracy, as predictive saccades are often hypometric (Bronstein & Kennard, 1987). A specific form of prediction is suggested to occur for

saccades to moving targets, where saccades need to take into account the ongoing motion of the target during saccade programming (discussed in Chapter 5). One task that is frequently used to investigate cognitive or top-down influences on saccadic eye movements is the anti-saccade task. In this task observers are asked to make a saccade opposite to the target, to its mirror position (Everling & Fischer, 1998; Munoz & Everling, 2004), and this task requires cognitive inhibition of a reflexive saccade towards the target, as well as the generation of a voluntary, cognitively-driven saccade in the opposite direction. Saccade inhibition is typically impaired in some psychiatric disorders, such as schizophrenia, obsessive-compulsive disorder, and attention-deficit/hyperactivity disorder (Levy et al., 2004).

In summary, saccadic eye movements are made in numerous different contexts and in response to a variety of different types of stimuli, although the underlying mechanisms and processes involved are believed to be very similar under all these conditions. The current thesis mainly investigates saccades to moving targets, and in particular saccades that occur during visual tracking. Saccadic and smooth pursuit eye movements work in synergy when visually tracking targets, although the mechanisms of this synergy are not yet clear (see Chapter 4). Furthermore, the saccadic component of visual tracking is frequently neglected in visual tracking research or reported inadequately. The aim of the current work was to investigate the role of saccades in visual tracking and better describe and quantify the saccadic tracking contribution as a function of slow, medium and fast target velocities.

Smooth pursuit eye movements

Introduction

Smooth pursuit eye movements are the smooth, conjugate movements of the eyes while keeping a moving object foveated to allow continuous viewing of the object. Non-primate species are also able to make smooth conjugate eye movements (e.g., rabbit, cat), but these result in movements of the whole visual field, while smooth pursuit in humans and primates is unique in that it allows pursuit of an object across a stationary background (Lisberger et al., 1987; Walls, 1962). Pursuit eye movements are usually considered voluntary eye movements (Pola & Wyatt, 1991) as observers can voluntarily pursue or ignore an object (Kowler, Van der Steen, Tamminga, & Collewijn, 1984), although they are sometimes described as a sensorimotor reflex (see Eckmiller, 1987; Kowler, 1990). Either way, they can generally not be performed in the absence of an adequate stimulus to be pursued (e.g., R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Kowler, 1990) and attempts to produce smooth movements without an adequate motion stimulus typically result in successive saccades (Lisberger et al., 1987).

Smooth pursuit eye movements are sometimes classified in regards to the stimulus used to evoke them in the laboratory. Popular stimuli are the *ramp stimulus* (a stationary stimulus suddenly starts to move smoothly in one direction), the *step-ramp stimulus* (Rashbass, 1961) (a stationary stimulus jumps in one direction and then immediately starts moving smoothly in the opposite direction) sinusoidal pursuit (a stimulus moving periodically in opposite directions across a trajectory, slowing in the

periphery and therefore producing a sine wave output), and linear pursuit (a stimulus moving periodically in opposite directions at a constant velocity, therefore producing a triangular wave output). Also, in the natural setting, smooth pursuit occurs in all directions and can even have curved trajectories, but in the laboratory, pursuit across only one dimension is typically investigated. Horizontal pursuit is investigated more frequently than vertical or diagonal pursuit and performance on horizontal pursuit tends to be superior (e.g., Collewijn & Tamminga, 1984; Rottach et al., 1996). Further, a distinction is usually made between the *open loop* and *closed loop* components of smooth pursuit eye movements. These components have been associated with quite different retinal events (Eckmiller, 1987; Lisberger et al., 1987), although there is no evidence that their responsiveness differs (M. M. Churchland & Lisberger, 2000). The open loop component is the initiation of pursuit: the first 100ms of the pursuit response to a new stimulus or a change in direction or velocity of a stimulus (Lisberger & Westbrook, 1985). During this time, the pursuit system functions without any feedback. Open loop pursuit can be further divided into early and late components (Gellman & Carl, 1985; Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986). The initial 20-40ms is only selective for direction and independent of stimulus characteristics with the aim of initiating a smooth eye movement in the required direction as soon as possible. Only during the later part of the 100ms period is the response affected by target velocity and stimulus position (eccentricity), which result in eye acceleration. Closed loop pursuit refers to the subsequent pursuit response when the system is under visual feedback control. This fully engaged pursuit response is also called *maintained* or *steady-state* pursuit. Open loop or pursuit initiation is often studied as a direct estimate of the input versus output of smooth pursuit (the forward path component of the pursuit system), without

'contamination' from visual feedback (Bahill & Harvey, 1986; R. H. S. Carpenter, 1988; Lisberger et al., 1987; Wyatt & Pola, 1983). Open loop conditions can be artificially produced by tracking the foveal afterimage, electronically moving a target along with the eyes or immobilising the stimulus in one eye and measuring the motion in the other eye. However, the study of the initial 100ms of normal pursuit is more natural (see Lisberger et al., 1987). Others have questioned the validity of using open loop as the main tool to study the pursuit system (e.g., Collewijn & Tamminga, 1986) and argue for studying the fully engaged pursuit system.

In addition to the above distinction, it is important to differentiate between single and dual-mode pursuit, as the eyes use both saccadic and smooth pursuit eye movements to track visual targets. Prior to 1980, when smooth pursuit eye movements were investigated, the whole tracking response was used to determine pursuit performance. Bahill, Iandolo, and Troost (1980), followed by others (Collewijn & Tamminga, 1984; Yasui & Young, 1984) realised the importance of separating the saccadic and smooth pursuit components of the tracking response and reporting them individually. They distinguished between *dual-mode pursuit* (tracking performance when saccadic and smooth pursuit responses are combined) and *single-mode pursuit* (smooth pursuit component only), and it is the single-mode pursuit response only that reflects the functioning of the pursuit system. Reporting only the dual-mode pursuit performance can actually contaminate the results by giving the impression of better than actual *smooth pursuit* tracking performance (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995), particularly for high target velocities (Bahill et al., 1980). Actually, a more accurate way of naming these is to call them dual-mode *tracking* and single-mode *pursuit,* to highlight that only the single-mode reflects the performance of smooth

pursuit eye movements, while dual-mode tracking is composed of both smooth pursuit and saccadic eye movements. These terms will be used throughout this thesis.

Parameters of smooth pursuit eye movements

The main measure used to describe smooth pursuit performance is pursuit gain (target velocity divided by eye velocity), which describes how well the eye velocity matches target velocity. Eye velocity is also often reported as a measure of pursuit, although by itself it does not indicate how well the eye matches target velocity, which is why gain is the preferable measure. Eye velocity during normal pursuit typically exhibits a degree of oscillation (e.g., see Pola, 2002). Smooth pursuit gain of 1.0 reflects perfect pursuit performance and, in optimal conditions, average pursuit gains of 0.9-0.95 have been reported (Schalen, 1980). Gain of 0.7 is considered to be the low end of normal pursuit for fast velocities [above 20 deg/s] (D. A. Robinson, Gordon, & Gordon, 1986), although pursuit gains ranging from 0.6-0.95 have been reported as normal (Pola, 2002). Gain greater than 1.0 indicates that the eye leads the target, which can occur, although it is more common that the eyes lag behind the target (Kowler, 1990; Pola & Wyatt, 1991), which makes sense given that smooth pursuit operates on a feedback system. Smooth pursuit performance can be enhanced with auditory, tactile, or proprioreceptive information (Ciuffreda & Tannen, 1995; Pola & Wyatt, 1991; Steinbach & Held, 1968), as well as with practice (R. H. S. Carpenter, 1988; Kowler, 1990; Madelain & Krauzlis, 2003; Schalen, 1980). Smooth pursuit is negatively affected by decreasing relative contrast (Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986) or absolute contrast (Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005) adding various backgrounds (Collewijn & Tamminga, 1984; Kowler, Murphy, & Steinman, 1978; Spering & Gegenfurtner, 2007a; Wyatt, Pola,

Fortune, & Posner, 1994; R. D. Yee, Daniels, Jones, Baloh, & Honrubia, 1983), decreasing target size or increasing trajectory amplitude (Leigh & Zee, 1999). However, the most important factor affecting pursuit performance is target velocity (Ciuffreda & Tannen, 1995; Collewijn & Tamminga, 1984; Lisberger et al., 1987; Lisberger & Westbrook, 1985; Meyer, Lasker, & Robinson, 1985; Schalen, 1980; Tychsen & Lisberger, 1986), and the literature invariably reports that pursuit gain decreases with increasing target velocity. Early research reported velocity saturation of pursuit at target velocities around 30deg/s (Rashbass, 1961; D. A. Robinson, 1965; Westheimer, 1954; Young, 1971), although they did indicate that the eye can track at faster velocities, but very inaccurately and with deteriorated visual acuity (Ludvigh & Miller, 1953, cited in Westheimer, 1954). Currently there is a general consensus that up to 30-40deg/s target velocity smooth pursuit is quite accurate and it becomes increasingly inaccurate at faster velocities (see Lisberger et al., 1987; Pola & Wyatt, 1991) The upper limit of pursuit varies greatly between individuals, but can be up to 80-180deg/s (Buizza & Ramat, 2005; Lisberger, Evinger, Johanson, & Fuchs, 1981; Meyer et al., 1985), although pursuing an object at high velocities comes at a cost in accuracy. The general idea is that with decreasing gain at higher velocities, the eyes lag behind the target, which results in a saccade to refoveate the stimulus (*catch-up* saccade), and smooth pursuit at faster velocities is therefore interspersed with a greater number and larger saccades (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Hallett, 1986; Lisberger et al., 1987; Pola & Wyatt, 1991; Schalen, 1980). Even though it is suggested that pursuit is specialised for slowly moving targets (e.g., Lisberger et al., 1987), to date there appears to be no research that has investigated the lower velocity limits of smooth pursuit. Most research uses velocities of 5.0-10.0deg/s at the low end of the spectrum. Murphy (1978) included target speeds just

under 1.0 deg/s and found that gain decreased for very slow velocities for one observer and increased for the other observer. Collewijn and Tamminga (1984) had minimum velocity of 1.7 deg/s and found higher gain with lower velocity. Churchland and Lisberger (2000) investigated pursuit initiation to apparent motion at velocities lower than 2.0 deg/s. However, they excluded these from their study stating that the traces were too variable and had too many saccades to conduct a reliable and valid analysis. Carl and Gellman (1987) with minimum velocity of 1.0-2.0 deg/s found that velocities below 5.0 deg/s were associated with slower pursuit acceleration and significantly higher latencies. Similarly, Spering, Kerzel, Braun, Hawken, and Gegenfurtner (2005) included target velocity of 1.0 deg/s and found slower pursuit acceleration and higher latencies, as well as larger position errors and lower gain, than at 8.0 and 15.0 deg/s. For smooth pursuit of apparent motion, Lamontagne (1973) suggested a theoretical lower limit, when flash rate is so low that it would no longer permit continuous tracking. Based on this it would be conceivable that continuous motion would also have a lower velocity limit, albeit at slower target speed than apparent motion. However, this has never been directly investigated.

Pursuit latency is another variable used to investigate pursuit performance. This can involve either pursuit onset latency, or latency to sudden changes in direction or velocity of a target. Pursuit latency can range from 80-150ms (Carl & Gellman, 1987; R. H. S. Carpenter, 1988; Lisberger & Westbrook, 1985; Pola & Wyatt, 1991; Rashbass, 1961), although it is generally close to 100ms (Carl & Gellman, 1987). Latency can be significantly reduced (to virtually zero latency) using highly predictable target waveforms (Bahill & McDonald, 1983; Westheimer, 1954). Pursuit latency has also been found to vary slightly with the luminance, size, and initial

position in the visual field of the target (Lisberger & Westbrook, 1985) and is longer for slow velocities (below 5.0 deg/s, Carl & Gellman, 1987).

Stimuli driving smooth pursuit eye movements

In a classic study, Rashbass (1961) used the step-ramp stimulus to investigate whether target position or target motion is the primary stimulus driving smooth pursuit. Although previous researchers had suggested that motion was the driving stimulus for pursuit, using this now famous paradigm, Rashbass demonstrated that when offered both stimuli, the initial smooth movement of the eye was dictated by the motion of the target, rather than the position displacement. In particular, as the velocity of the eyes is linearly related to target velocity of the stimulus, target velocity (through retinal slip velocity) was originally seen as the main stimulus driving smooth pursuit movements (Rashbass, 1961; D. A. Robinson, 1965; Young, 1971; Young & Stark, 1963), with position errors compensated exclusively by saccades (e.g., Rashbass, 1961; Westheimer, 1954). Whereas target velocity relative to the retina is still considered a primary stimulus for smooth pursuit (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Eckmiller, 1987; Pola, 2002; Pola & Wyatt, 1991), target acceleration has more recently also been identified as an important input to the pursuit system (Lisberger et al., 1981; D. A. Robinson et al., 1986). However, while Rashbass's original paper discounted a position signal as a stimulus for pursuit, over the years there has been increasing evidence of a position input to the pursuit system. This includes evidence that after-images can be smoothly pursued (Heywood & Churcher, 1971) and evidence of a smooth pursuit response to position signals during open-loop and closed-loop smooth pursuit in humans (Carl & Gellman, 1987; Pola & Wyatt, 1980; Tarnutzer, Straumann, & Zee, 2007; Wyatt & Pola, 1981) and in

monkeys (Morris & Lisberger, 1987; Neary, Pola, & Wyatt, 1985, 1987). Furthermore, findings from various studies investigating pursuit of apparent motion (using series of stationary signals to elicit pursuit; Heywood, 1973; Morgan & Turnbull, 1978; Pola & Wyatt, 1980; Wyatt & Pola, 1981, see Chapter 4), have been interpreted as evidence for a position input to the pursuit system. Carpenter (1988) proposed that the position signal may provide the visual system with a qualitative signal relating to *which* cells are active at any given time, while the velocity signal information consists of a quantitative signal regarding *how much* cells are firing. Pola and Wyatt (1991) suggested that the position signal may be more important when close attention is paid to the pursued target, or during pursuit termination (Pola & Wyatt, 2001). However, there are some who question the idea that position information provides any input at all (Kowler, 1990). The predominant current view is that the pursuit system functions using multiple inputs, including velocity, acceleration, and position information (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Eckmiller, 1987; Lisberger et al., 1987; Pola & Wyatt, 1991).

Some of the evidence for a position input in smooth pursuit (e.g., Behrens & Grüsser, 1979; Bridgeman, 1989; Heywood & Churcher, 1971; Pola & Wyatt, 1980; Wyatt & Pola, 1981) has also been cited as evidence for an alternative view; conceptualising *perceived* motion or *perceived* velocity as the primary stimulus driving pursuit (R. H. S. Carpenter, 1988; Krauzlis & Stone, 1999). Further evidence for this notion includes pursuit of afterimages in the absence of actual target motion (Braun, Pracejus, & Gegenfurtner, 2006; Yasui & Young, 1975), pursuit of extra-foveal targets (e.g., Collewijn & Tamminga, 1986), and pursuit of illusionary targets (Madelain & Krauzlis, 2004; Steinbach, 1976), as well as imaginary targets (Deckert,

1964; Ilg & Thier, 1999; Wyatt et al., 1994). There is also evidence that the pursuit response is more closely related to perceived rather than actual target velocity when the two are different (Pola & Wyatt, 1980; Wyatt & Pola, 1979), and that pursuit is more related to perceived motion than image motion when they differ (Beutter & Stone, 2000; Stone, Beutter, & Lorenceau, 2000). However, opponents of this view have dismissed such findings by suggesting that they have been obtained with unusual stimuli or are based on prediction/observer expectation (Kowler, 1990), or use peripheral tracking (Hallett, 1986), and that if observers are presented with differences in perceived and actual motion, then the eye will pursue the actual motion (Mack, Fendrich, & Pleune, 1979; Mack, Fendrich, & Wong, 1982). Kowler (1990) stated that while humans pursue a highly organised motion signal, observers do not actually pursue what they perceive. However, in natural viewing conditions perceived and retinal motion are not usually in conflict. Pola and Wyatt (1991) suggested that perceived motion might function to supplement retinal target motion, particularly when the target motion signal is weak. In order to do so the visual system can utilise various cues, including extrafoveal (Wyatt et al., 1994) and proprioreceptive (Gauthier & Hofferer, 1976; Steinbach & Held, 1968) information. However, more recent research (outlined in Chapter 3) into the possibility of shared processes of motion perception and smooth pursuit eye movements is providing further evidence that perceived motion could be a main driving stimulus for smooth pursuit eye movements.

Models of the smooth pursuit system

Aside from the question of *what* is being pursued by the smooth pursuit system, the question of *how* the pursuit system works has also been extensively investigated.

Rashbass (1961) originally suggested that, once pursuit was initiated by motion across the retina and target velocity was reached, the eye would remember the velocity and maintain smooth pursuit at that velocity until a change in target motion occurred (based on the Craik, 1947 model of manual tracking). Yet this was inconsistent with the fact that the eyes generally lagged behind the target (Kowler, 1990), as well as with the small but continual oscillations of eye velocity during pursuit (Lisberger et al., 1987). Subsequent models of the pursuit system (Stark, Vossius, & Young, 1962; Young & Stark, 1963) recognised that visual information was continuously available to the pursuit system; therefore working under *negative feedback control* (Figure 3A). Such a negative feedback control system works by comparing input and output with the aim of reducing the difference between the two (Wyatt & Pola, 1983). The Young and Stark model conceptualised the pursuit system as a basic velocity servomechanism, with the aim of matching eye velocity to target velocity and reducing retinal image motion (target velocity minus eye velocity) to a minimum. However, there were two major problems with this model. Firstly, perfect velocity matching would result in a zero velocity error and therefore no feedback signal and no pursuit, and secondly, with a 100ms processing delay the system would become unstable (Lisberger et al., 1987). Revised internal feedback control models solved these problems by proposing the existence of a 'reconstructed' velocity signal in which the addition of eye velocity and retinal target velocity become the input to the pursuit system (D. A. Robinson, 1971; Young, 1971). In addition to the negative feedback for visual information, Yasui and Young (1975) and Robinson (1965; D. A. Robinson et al., 1986) proposed the addition of an internal *positive* feedback loop of the motor command for pursuit eye velocity that is independent of the negative feedback loop (Figure 3B). Subsequent models of the pursuit system (Lisberger et al.,

1987) have been further expanded by adding information regarding retinal velocity errors, as well as retinal position and retinal acceleration errors as inputs to the system. Their model still includes an internal feedback loop and a eye velocity positive feedback loop, but Krauzlis and Lisberger (1994) have called their model an *image motion model*, to distinguish it from previous *internal feedback models* (D. A. Robinson et al., 1986). In image motion models the dynamics of eye velocity emitted by the model are determined by visual inputs (generally retinal slip), whereas in internal feedback models they are produced by the internal feedback loop.

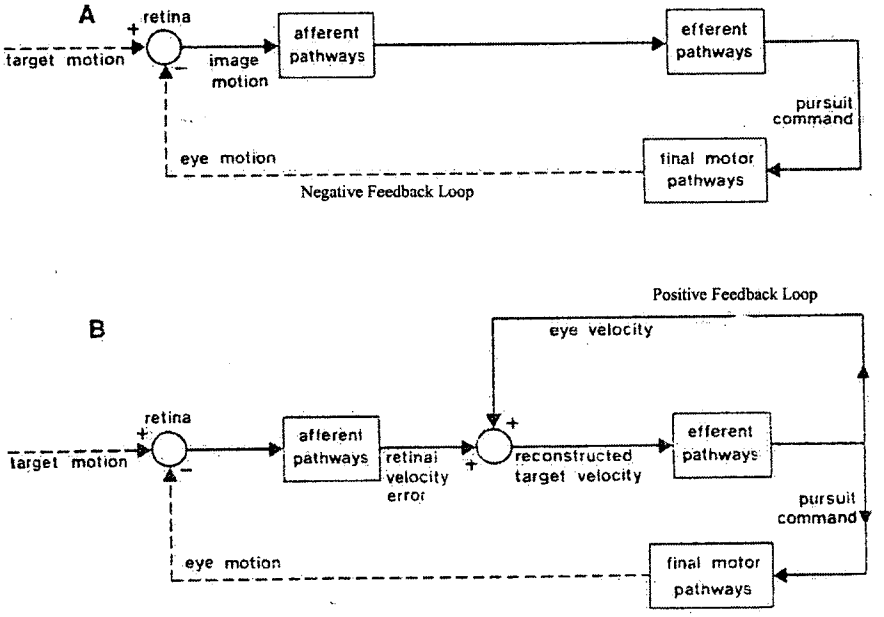

Figure 3. Two basic models of the smooth pursuit system. **A** illustrates a simple negative feedback system with image motion as the main signal. **B** illustrates a modification including a positive feedback loop for the smooth pursuit eye velocity signal. Reconstructed target velocity is computed from the added inputs of retinal velocity error and eye velocity feedback (from Lisberger et al., 1987, p. 103).

A further component of the smooth pursuit system was proposed by Lisberger and colleagues (Krauzlis & Lisberger, 1994; Lisberger et al., 1987): *eye velocity memory*. In addition to the negative feedback loop, it has been found that even when retinal errors are prevented by image stabilisation, eye velocity is maintained by the pursuit

system (Morris & Lisberger, 1983). Eye velocity memory was suggested as a neural velocity memory that sustains pursuit velocity in the absence of retinal errors, and it has been included in many models of smooth pursuit. Even though existing models of the pursuit system have been found to describe pursuit performance quite accurately (Ciuffreda & Tannen, 1995; Krauzlis & Lisberger, 1994) they do not account for or fail to address a number of factors. This includes the influence of cognitive factors, such as attention, the predictive properties of pursuit, the influence of perception, and the mechanisms of saccadic and pursuit eye movements in tracking (Pola & Wyatt, 1991).

Cognitive factors in smooth pursuit eye movements

Cognitive factors play an important role in smooth pursuit eye movements (Barnes, 2008; R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Horii, 1994; Kowler, 1990; Lisberger et al., 1987) and this role is reflected in the distinction that is sometimes made between retinal (derived from image motion) and extraretinal inputs to the pursuit system (Barnes, 2008; Barnes & Asselman, 1991; Bennett & Barnes, 2003; Krauzlis & Miles, 1996a; Leigh & Zee, 1999). The extraretinal signals include cognitive variables, such as expectation, attention, and memory. One feature of smooth pursuit that has contributed significantly to investigating extraretinal inputs is prediction. Prediction is the pursuit system's ability to use information about past motion (Stark et al., 1962) to anticipate changes in the position or velocity of a target (Boman & Hotson, 1992; Kowler & Steinman, 1979). For example, it has been shown that periodic or predictable stimulus motion is tracked more accurately than irregular or unpredictable motion (e.g., Bahill et al., 1980; Dodge, Travis, & Fox, 1930) and that pursuit of predictable stimuli has a shorter onset latency and almost no latency to

predictable changes in velocity or direction (e.g., Bahill & McDonald, 1983; Westheimer, 1954; Whittaker & Eaholtz, 1982). Furthermore, the system can even anticipate the onset of a ramp and step-ramp motion with very slow smooth eye movements (typically below 1 deg/s) in the direction of the motion starting before the target moves, and these are called anticipatory eye movements (Boman & Hotson, 1988, 1992; Kowler & Steinman, 1979). These anticipatory eye movements generally depend on recently encountered target motion (Kowler, 1989; Kowler, Martins, & Pavel, 1984), are stimulus dependent, and driven by perceived motion (Boman & Hotson, 1988, 1992). It was initially questioned whether anticipatory eye movements were a component of prediction, but Boman and Hotson (1992) found that predictive eye movements associated with abrupt changes in target motion actually consisted of a number of anticipatory movements. They concluded that anticipatory eye movements constitute a fundamental component of prediction. In recognition of the role of prediction, it is frequently recommended that unpredictable target motion should be used when investigating pursuit (e.g., Bahill et al., 1980; R. H. S. Carpenter, 1988). On the other hand, it has been questioned whether a truly unpredictable target exists (Becker & Fuchs, 1985; Pavel, 1990) because it has been shown that observers attempt to make predictions even in response to unpredictable targets (Yasui & Young, 1984). If this is the case, then with more periodic stimuli at least the predictive component is less variable and may even be constant.

Prediction is also involved in the ability of the pursuit system to bridge a visual gap during brief target disappearance (also called *continuation*, Pola & Wyatt, 1991) (Becker & Fuchs, 1985; Bennett & Barnes, 2003, 2004; Eckmiller & Mackeben, 1978; Madelain & Krauzlis, 2003; Von Noorden & Mackensen, 1962; Whittaker &

Eaholtz, 1982). When a target briefly disappears during pursuit, the eye can maintain eye velocity and is able to follow previously used trajectories, and can even produce smooth changes for up to 1,000ms in humans (Von Noorden & Mackensen, 1962; Whittaker & Eaholtz, 1982) and in monkeys (Eckmiller & Mackeben, 1978), provided observers expect it to reappear. A classic study by Becker and Fuchs (1985) found that observers were indeed able to bridge gaps in target motion, although they found that eye velocity did start to decelerate rapidly 200ms after target disappearance. Interestingly, they found that this deceleration had a consistent pattern, with eye velocity reaching a residual velocity of up to 60% of target velocity by 450ms after target disappearance, which could be maintained for a minimum of 4,000ms. In addition, Bennett and Barnes (2003, 2004) found anticipatory acceleration of eye velocity before target reappearance, and also found that saccades were triggered after target disappearance, generally placing the eye slightly ahead of the occluded target (Bennett & Barnes, 2006).

These observed predictive phenomena suggest that the pursuit system does not merely respond to the retinal motion stimulus, but includes several kinds of internal signals in order to compensate for the reactive and delayed response to visual feedback (Bennett & Barnes, 2003; Kowler & Steinman, 1979). However, if predictive and actual visual signals are in conflict, the system will use the visual inputs to drive pursuit (Barnes & Asselman, 1991). Early explanations for prediction were that it was the result of higher level cognitive processes superimposed on the basic pursuit system mechanisms (Stark et al., 1962; Westheimer, 1954). In contrast, others consider these predictive properties an inextricable part of the pursuit system (Becker & Fuchs, 1985; Kowler & Steinman, 1979; Pavel, 1990; Pola & Wyatt,

1991) that need to be included in any complete model of the pursuit system (see Pavel, 1990, for a detailed review of prediction and oculomotor models). Lisberger and colleagues' concept of eye velocity memory (Krauzlis & Lisberger, 1994; Lisberger et al., 1987) provides a possible explanation for continuation, but it is unable to account for other aspects of prediction, such as predictive *changes* in velocity or direction. Barnes and colleagues (Barnes & Asselman, 1991; Barnes, Barnes, & Chakraborti, 2000; Barnes & Doneland, 1999) have suggested that predictive eye movements are based on stored estimates of both timing and eye velocity, obtained from observed motion over a few cycles. In this context, Pavel (1990) distinguishes between two different types of prediction: prediction of future motion based on previous target motion and prediction based on cognitive decision-making processes using contextual cues and observer knowledge. This proposal is similar to the view of Kowler and colleagues (Kowler, 1990; Kowler, Martins et al., 1984), who suggested that prediction is dependent to some degree on past history of the pursued motion but, more importantly, on cognitive expectations.

In addition to prediction, another important cognitive factor in smooth pursuit is attention (Hoffman, 1998), although the term *attention* is generally used very loosely. It has been stated that attention instructions have no significant effect on pursuit performance (Sperling, 1990), although others have found that active, attentive pursuit can significantly increase gain compared with passive viewing (Pola & Wyatt, 1991). The notion that attentional processes are an important aspect of smooth pursuit is consistent with brain imaging studies finding overlap in the active neurological areas associated with attention and pursuit eye movements (Corbetta et al., 1998; Culham et al., 1998). Visual attention determines whether a target is pursued or

ignored (Kowler, Van der Steen et al., 1984) and which target is selected for pursuit (Kowler, 1990). Further, pursuit performance has been shown to decrease when visual attention had to be shared with visual perception tasks (Khurana & Kowler, 1987). Also, Puckett & Steinman (1969) demonstrated that practised observers could choose to either match velocity or maintain minimum fixation error when tracking a target. Furthermore, parallel studies investigating attentive tracking found very smooth attentional shifts during attentive tracking and remarkable similarities between pursuit and visual attention (see Shioiri, Yamamoto, Kageyama, & Yaguchi, 2002).

The current research investigates the visual stimuli that elicit and drive smooth pursuit by separating the position and velocity input signals to create a range of target stimulus velocities in order to study the lower velocity limits of smooth pursuit and how saccadic and smooth pursuit eye movements work together during visual tracking.

Chapter 3

The neurology of eye movements

The neuro-anatomy of eye movements

Introduction

Given that eye movements are simpler than many other human movements, the oculomotor system provides an excellent opportunity to investigate the neurological processes involved in visually guided movements in general (Keller & Heinen, 1991; Leigh & Zee, 1999; Lisberger et al., 1987; D. A. Robinson, 1986) and it is partly for this reason that the neurology of oculomotor activity has been so extensively studied (Eckmiller, 1987). The main structures in eye movements involve both subcortical and cortical areas. Important subcortical structures include areas of the brainstem, midbrain, basal ganglia, and the cerebellum, although the thalamus has also been implicated. Cortical structures include striate and extrastriate visual areas, posterior parts of the parietal cortex, as well as some frontal cortical areas, particularly the frontal eye field (FEF). While saccadic and smooth pursuit eye movements are generally believed to be driven by different neurological processes (Bach-y-Rita, 1973; Lisberger et al., 1987; Rashbass, 1961) there is some overlap in the involvement of structures and pathways (Krauzlis, 2004, 2005). Although this thesis does not directly investigate neurological structures, a basic understanding of the neurology of eye movements is important when studying oculomotor activity. The present chapter describes the roles and interactions of the neurological structures that are involved in saccadic and smooth pursuit eye movements. Available evidence

regarding the neurology of eye movements comes predominantly from studies with primates, but research with monkeys has direct applicability to understanding the generation of eye movements in man (Keller & Heinen, 1991; Wurtz, 1996). More recently the advances in neuroimaging techniques and clinical studies have provided corroborative evidence for these findings in human observers.

Subcortical structures

The brainstem, which is made up of the pons, the midbrain (or mesencephalon) and the medulla, is the lowest neurological structure involved in eye movements. The pons and the medulla, contain numerous nuclei, several of which are involved in saccadic and smooth pursuit eye movements (Hepp et al., 1989; Keller, 1991). The inputs to the various brainstem nuclei vary, but include pathways from the superior colliculus and the FEF, and some of the nuclei are interconnected with the cerebellum and each other. However, the most important output of the brainstem nuclei involved in eye movements is to the three ocular cranial nuclei, which innervate the three muscle pairs and transmit the final commands to the extraocular muscles to move the eyes. The effects of brainstem lesions depend on the specific location (i.e., which of the nuclei are affected) and can have profound effects on the associated eye movements. Traditionally, distinct brainstem regions were associated with saccadic and pursuit eye movement, although this clear separation has been somewhat challenged in recent years (see Krauzlis, 2004, 2005).

The midbrain is made up of various structures involved in the generation of eye movements, including the superior colliculus and the substantia nigra. The superior colliculus is one of the most crucial structures for saccadic eye movements (Wurtz,

1996), and although it has recently been shown to be active during pursuit eye movements (Basso, Krauzlis, & Wurtz, 2000; Krauzlis, 2001; Krauzlis, Basso, & Wurtz, 2000; Krauzlis & Dill, 2002), it is traditionally associated with saccadic eye movements (Eckmiller, 1987). The superior colliculus can be divided into superficial, intermediate and deep layers, with quite different functions (see Guitton, 1991). The superficial layers (D. A. Robinson & McClurkin, 1989) are primarily visual and receive direct inputs from the retina and the visual cortex, as well as the FEF. They are interconnected with the deep layers and other brainstem structures and also project to the thalamus. The intermediate and deep layers (Sparks & Hartwich-Young, 1989) have a central role in sensorimotor integration, and are believed to transform sensory signals into motor commands for orienting responses. These deeper layers have more complex interconnections with other sites, and are therefore believed to be a site for convergence of multi-modal sensory information. This includes inputs from the substantia nigra, the thalamus, and the cerebral cortex (including the FEF). The deep layers are interconnected with the cranial nuclei in the pons and medulla responsible for innervating the oculomotor muscles. The superior colliculus therefore functions as an integrative structure between cortical and subcortical signal processing and the brainstem premotor circuit in saccade generation (Trappenberg, Dorris, Munoz, & Klein, 2001). Even though the superior colliculus is such an important structure in saccade generation, deficits associated with lesions to this area are generally mild and often temporary (Guitton, 1991; Sparks & Hartwich-Young, 1989). Such lesions generally result in increased saccade latency, a decrease in frequency, velocity, and accuracy of saccades (Sparks, 1986), and difficulties with target selection (McPeek & Keller, 2004). Lesions of the superior colliculus also affect the metrics of smooth pursuit (Basso et al., 2000), as well as target selection

(Nummela & Krauzlis, 2008a) and the contribution of visual stimuli to smooth pursuit eye movements (Nummela & Krauzlis, 2008b).

The substantia nigra is anatomically a midbrain structure, but is generally associated with the basal ganglia (Gray et al., 2005). The basal ganglia are a group of five nuclei, two of which, the caudate nucleus and the substantia nigra, play a role in oculomotor control. The basal ganglia has traditionally been associated with saccadic eye movements (see Guitton, 1991; Hikosaka & Wurtz, 1989), but has more recently it has been found to play a role also in pursuit (O'Driscoll et al., 2000; Pokorny & Basso, 2003). The caudate nucleus receives input from the thalamus and the cerebral cortex (parietal areas, prefrontal area, FEF, and temporal areas) and has an inhibitory connection to the substantia nigra. The substantia nigra (in particular the substantia nigra reticular formation) in turn has an inhibitory connection with the superior colliculus. Increased activity in the caudate nucleus therefore inhibits the tonic firing of the substantia nigra, releasing its inhibition of the superior colliculus. Lesions to the caudate nucleus or the substantia nigra, or disease affecting the basal ganglia, such as in Parkinson's or Huntington's disease, all affect oculomotor activity (Hikosaka & Wurtz, 1989; Leigh & Zee, 1999). Lesions to the substantia nigra also result in degeneration of the superior colliculus (Hikosaka & Wurtz, 1989), which in turn also affects saccadic eye movements.

Another important subcortical structure is the cerebellum, which is involved in the control of all oculomotor activity in mammals, although different regions have been implicated in different types of eye movements (Keller, 1989; Leigh & Zee, 1999; F. A. Miles, 1991; F. R. Robinson & Fuchs, 2001). The cerebellum is made up of two

hemispheres divided by the vermis (Gray et al., 2005), which has been mainly associated with saccadic eye movements (McElligott & Keller, 1984). Other structures of the cerebellum that are important for oculomotor activity are a pair of small lobes on the posterior border, the flocculus and paraflocculus, which have been shown to play a greater role in smooth pursuit (Sato & Noda, 1992). Input to the cerebellum is via mossy, or climbing, fibres and the only output of the cerebellum is via the Purkinje cells, which make up the middle layer of the cerebellar cortex. The cerebellum receives inputs from many cortical and subcortical regions, including brainstem circuits. The cerebellum mainly has a modulatory function in eye movement control (Keller, 1989; F. A. Miles, 1991), which means that it is important for the control, rather than the generation of eye movements (F. R. Robinson & Fuchs, 2001). In saccades the cerebellum ensures saccade accuracy over time (Keller, 1989), and cerebellar lesions or disease therefore affect saccades only by making them less accurate and more variable in size and speed (Ritchie, 1976; F. R. Robinson & Fuchs, 2001; F. R. Robinson, Straube, & Fuchs, 1993). In smooth pursuit, the cerebellum provides more ongoing and essential inputs (Krauzlis & Lisberger, 1991; F. A. Miles, 1991), playing a significant role in the control of both predictive and visually guided smooth pursuit (Suh, Leung, & Kettner, 2000), and possibly being involved in the positive feedback loop for pursuit eye velocity (Lisberger et al., 1987). Cerebellar problems therefore profoundly affect or even abolish pursuit eye movements (F. A. Miles, 1991), with lesions to several areas of the cerebellum impairing pursuit initiation and gain (Straube, Scheuerer, & Eggert, 1997; Vahedi, Rivaud, Amerenco, & Pierrot-Deseilligny, 1995; Zee, Yamasaki, Butler, & Gücer, 1981).

The thalamus is a less important oculomotor structure, but it does play a role in eye movements, as many cortical signals are relayed through this area (e.g., Eckmiller, 1987). The main areas of thalamus involvement in oculomotor activity are the central thalamus (Schlag-Rey & Schlag, 1989) and the pulvinar (D. A. Robinson & McClurkin, 1989). The thalamic structures receive inputs from the parietal cortex, the FEF, and the superior colliculus and project back to the visual, temporal, and frontal cortices. Their precise role in oculomotor control is not fully established but mainly involves visual attention for salient or sudden events (Michael & Buron, 2005; Petersen, Robinson, & Keys, 1985; D. L. Robinson & Petersen, 1992). Lesions to the thalamic structures affect shifts in attention and gaze, as well as saccade accuracy and latency (Leigh & Zee, 1999).

Cortical structures

As for the cerebral cortex, there are many cortical areas involved in the generation and control of saccadic and smooth pursuit eye movements. This is consistent with oculomotor activity involving a number of high-level processing tasks, including target selection, attention, memory, cognitive decision-making, and learning (see Fischer & Boch, 1991, for a review on cortical oculomotor contol). The first cortical region involved in oculomotor control is the visual cortex (including striate and prestriate areas) which receives its input from the retina via the lateral geniculate nucleus (LGN). The striate cortex (V1) is interconnected with the pontine and medullary cranial nuclei and is heavily connected to the superior colliculus. It also projects to other visual areas, including the prestriate (V2, V3, V4) and extrastriate (e.g., medial temporal area, MT, and medial superior temporal area MST) cortices. The striate and prestriate areas (particularly V1 and V2) provide the visual input

signals driving eye movements, although the precise function of the prestriate areas is not very well established (Fischer & Boch, 1991), while area V4 has also been tentatively linked to selective attention (see Eckmiller, 1987). Lesions to the striate cortex impair saccades in the visual area affected by the lesion (Fischer & Boch, 1991). Unilateral lesions affect pursuit eye movement in the corresponding visual hemisphere (Goldberg, Bruce, Ungerleider, & Mishkin, 1982), while bilateral lesions abolish pursuit eye movements (Miller, Pasik, & Pasik, 1980).

Extrastriate areas, such as the temporal areas MT (human V5) and MST (human V5a), are also important in oculomotor activity. Because of their crucial function in motion processing MT and MST are important for pursuit eye movements (Ilg, 2008) and, in addition, they are also involved in saccade generation to moving targets (Krauzlis & Stone, 1999; Newsome, Wurtz, Dürsteler, & Mikami, 1985). MT is interconnected with MST and projects to the FEF, pontine nucleus and the superior colliculus. MST has reciprocal connections with the FEF and area 7 of the parietal cortex. Areas MT and MST are direction selective and show strong activation during smooth pursuit (Bremmer, Ilg, Thiele, Distler, & Hoffmann, 1997; Komatsu & Wurtz, 1988). Neurons in MT are only active when there is an actual visual stimulus, while MST neurons are also active in the absence of visual stimuli, as found during target blanking and image stabilisation (Ilg, 2003; Nagel et al., 2006; Newsome, Wurtz, & Komatsu, 1988). This indicates that MT responds only to retinal signals, while MST receives both retinal and extraretinal inputs. It has been suggested that the extraretinal signal consists of an efference copy of eye velocity (Newsome et al., 1988; Pack, Grossberg, & Mingolla, 2001). Cells in MT are also tuned for velocity (Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983a) and it has been

proposed that MT provides the velocity signal for pursuit initiation based on target motion speed (Lisberger & Movshon, 1999; Priebe, Churchland, & Lisberger, 2001). Lesions in MT and MST cause profound pursuit deficits (Dürsteler & Wurtz, 1988), but monkeys can continue to produce pursuit in response to position information (Dürsteler, Wurtz, & Newsome, 1987) and they recover from MT/MST lesions within a few days (Yamasaki & Wurtz, 1991). This indicates that even though MT and MST are important components of the smooth pursuit system, they are not essential for the production of smooth pursuit (Keller & Heinen, 1991) because alternative inputs and pathways can provide a substitute mechanism. With regard to saccadic eye movements, lesions to MT and MST did not alter saccades to stationary targets but they impaired saccade accuracy to moving targets (Newsome et al., 1985).

Areas of the frontal cortex have also been implicated in oculomotor control, particularly the FEF, which is important for both saccadic and smooth pursuit eye movements (Lencer & Trillenberg, 2008; McDowell, Dyckman, Austin, & Clementz, 2008). The FEF is active before the initiation of purposeful, but not spontaneous, saccades (Fischer & Boch, 1991; Gaymard, Lynch, Ploner, Condy, & Rivaud-Péchoux, 2003; Goldberg & Segraves, 1989). This indicates that the FEF plays a role in cognitively driven saccades (Guitton, 1991; Pierrot-Deseilligny, 1994). The FEF has also been suggested as the site for visual target selection for saccades (Schall, 2002; Schall & Hanes, 1998; Schall & Thompson, 1999; Schiller & Chou, 1998). The FEF is also involved in smooth pursuit eye movements, although it is spatially and structurally different part of the FEF, often referred to as the *frontal pursuit area*, FPA (Chou & Lisberger, 2004; A. K. Churchland & Lisberger, 2005; Gagnon, Paus, Grosbras, Pike, & O'Driscoll, 2006). It has been shown that parts of the FEF are

active during smooth pursuit (Gottlieb, MacAvoy, & Bruce, 1994; Kawawaki, Shibata, Goda, Doya, & Kawato, 2006; MacAvoy, Gottlieb, & Bruce, 1991; Ohkubo et al., 2000; Petit & Haxby, 1999; Pierrot-Deseilligny, 1994) and play a particular role in pursuit initiation (Drew & van Donkelaar, 2007), pursuit prediction (Lencer, Nagel et al., 2004; Nagel et al., 2006), and learning in pursuit (Chou & Lisberger, 2004). The FEF receives input from the visual and parietal cortices and is interconnected with the thalamus and the brainstem circuitry. It has direct connections to the superior colliculus, as well as indirectly via the basal ganglia. The FEF therefore has a sensory, as well as a motor component (Schall, 2002), and is believed to process both retinal and extraretinal signals (Ilg & Thier, 2008). Lesions to the FEF cause only short-term disruptions to saccade generation for normal saccades, including saccade latency and accuracy, as well as frequent intrusive saccades during fixation (Sommer & Tehovnik, 1997). In contrast, lesions to the FEF result in permanent impairments of saccades that have a cognitive component, including anti-saccades, saccades in response to verbal instructions, or remembered targets (Goldberg & Segraves, 1989), as well as the temporal ordering of saccades (Schiller & Chou, 1998). Furthermore, lesions to the FPA result in profound and lasting pursuit deficits, particularly the loss of predictive pursuit (Keating, 1991; Keating, Gooley, & Kenney, 1985; MacAvoy et al., 1991).

Another frontal region that has been implicated in oculomotor control is an area in the dorsomedial frontal cortex; the supplementary eye field (Lencer & Trillenberg, 2008). Initially the supplementary eye field was believed to be the oculomotor equivalent of the supplementary motor area (Schlag & Schlag-Rey, 1987), due to its location anterior to it. Cells in this area are active during pursuit (e.g., Petit & Haxby, 1999)

and just prior to saccadic eye movements (Schlag & Schlag-Rey, 1987). However, other findings have indicated that these cells are only active for saccades associated with specific learned or complex motor tasks (Fischer & Boch, 1991; Leigh & Zee, 1999). Nevertheless, the supplementary eye fields have many cells similar to the FEF and the superior colliculus and clearly play a role in saccade generation (Russo & Bruce, 2000), possibly in the ordering of consecutive saccades (Tobler & Müri, 2002), as a clear cognitive component to their functioning has been shown (Kennard et al., 2005). The supplementary eye field receives inputs from MST and is interconnected with the FEF and the parietal cortex and projects to the thalamus. Lesions to this area cause mild increase in saccade latency and saccade sequencing, although these have been found to be less profound than similar FEF lesions (Schiller & Chou, 1998).

Areas of the parietal cortex have also been found to play an important role in oculomotor activity, particular regarding visual attention, spatial perception and spatial orientation (Eckmiller, 1987; Keller & Heinen, 1991). Parietal areas therefore play an important role in saccades made to visual targets (R. A. Anderson & Gnadt, 1989), and in the generation of smooth pursuit (Fischer & Boch, 1991; Sharpe, 1998). Parietal areas are active in response to both visual stimuli, as well as during the associated eye movements, and therefore carry both sensory and motor signals, suggesting a sensorimotor integration role of the parietal cortex (R. A. Anderson & Gnadt, 1989; Kawawaki et al., 2006). In particular, area 7a and the lateral and ventral interparietal areas LIP and VIP (human analogue of LIP is sometimes called the parietal eye field, PEF; Müri et al., 1996) have been associated with eye movements (Petit & Haxby, 1999). Parietal areas receive input from the striate and extrastriate

cortices, and are interconnected to the FEF. They project directly to the superior colliculus and the brainstem circuitry. 7a, VIP and LIP/PEF have neurons that show saccade related activity (R. A. Anderson & Gnadt, 1989), as well as pursuit related activity (Ohkubo et al., 2000) and they contain cells which are direction selective and velocity tuned (Bremmer, Distler, & Hoffmann, 1997). LIP/PEF respond more strongly to new, unexpected, or salient stimuli (Gottlieb, Kusunoki, & Goldberg, 1998) whether or not an actual eye movement is made, indicating that this area is involved in the attentional shift necessary to make orienting or visually guided eye movements (Gaymard et al., 2003). This is consistent with parietal lesion showing saccadic deficits for tasks requiring unpredictable saccades, while predictable or memory-guided saccades are unimpaired (Gaymard et al., 2003). LIP has been associated with perceptual decision-making regarding visually guided movements (Shadlen & Newsome, 1996, 2001). Pursuit eye movements are also affected by parietal lesions (Barton & Sharpe, 1998), but due to the multiple cortical inputs to the pursuit system there is usually rapid recovery (Lisberger et al., 1987; Lynch & McLaren, 1982).

In summary, a number of cortical and subcortical structures are involved in the generation and control of saccadic and smooth pursuit eye movements. While some neuro-anatomical structures have traditionally been more clearly associated with either saccades or smooth pursuit, more recent research indicates that many of them play a role in both types of eye movements, although not necessarily to the same extent.

Traditional pathways for saccades and smooth pursuit

Neurological pathways for saccades

The neural processes involved in the generation of saccadic eye movements are quite complex and involve multiple parallel pathways. For visually guided saccades, all pathways start in the visual cortex, with the processing of the visual stimulus, and the final step of all routes is the brainstem circuitry (see Hepp et al., 1989). In between, however, there are multiple routes from the visual cortex to the brainstem, and this is why lesions to intermediate structures often do not abolish all saccades and have only short-term or milder effects on saccade generation. There is a direct route from the visual cortex to the superior colliculus and brainstem circuit (Figure 4A 1), which results in fast, visually guided saccades (Guitton, 1991). Another pathway is via the FEF (Figure 4A 2). From there multiple routes are possible: either directly to the brainstem nuclei (A 2a) or indirectly through the superior colliculus- with (A 2b) or without (A 2c) crossing the basal ganglia. The route including the FEF is mainly involved in more purposeful, volitional saccades with a clear cognitive component (Guitton, 1991; Pierrot-Deseilligny, 1994). A further route has also been suggested, from the visual cortex via the parietal cortex (LIP/PEF) to the superior colliculus (Figure 4A 3) and brainstem, with a main role in reflexive saccades to novel or salient visual stimuli (Gaymard et al., 2003). Obviously, other brain structures previously mentioned (e.g., thalamus) interconnect with these main routes at various locations and therefore mediate saccade generation. Once the signal arrives in the brainstem, the main areas involved in horizontal saccade generation are the paramedian pontine reticular formation (PPRF), which contains the excitatory burst neurons and the

omnipause neurons (see Chapter 2) and the dorsal medullary reticular formation (dMedRF), which contains inhibitory burst neurons (Hepp et al., 1989). Their activity result in the final pulse-step, which is transmitted to the motoneurons of the cranial nuclei, separately for each eye (Zhou & King, 1998), and mediated by the vestibular nuclei and the cerebellum.

Neurological pathways for smooth pursuit

The smooth pursuit pathway is often described as being somewhat simpler in comparison with the saccadic pathway, but despite its supposed simplicity Figure 4 illustrates that it embodies multiple pathways. The smooth pursuit system receives input from the motion processing pathways at numerous levels (Ciuffreda & Tannen, 1995) and is very closely linked with visual motion processing (Keller & Heinen, 1991). This relationship is discussed in detail in Chapter 5. Signals for pursuit eye movements start in the visual cortex (V1 and V2), as motion needs to be perceived for pursuit to be generated. One pathway (Figure 4B 1) proceeds from the visual cortex to areas MT/MST, and through parietal areas (i.e., 7a, LIP/VIP) and frontal areas (mainly FEF) to the pontine nuclei of the brainstem, which are involved in the generation of pursuit and include the dorsomedial pontine nucleus (DMPN), the dorsolateral pontine nuclei (DLPN), and the reticularis tegmentic ponti (NRTP). The other pathway (Figure 4B 2) bypasses areas MT/MST connecting directly via the parietal and frontal areas to the pontine nuclei. From any of these pontine nuclei, all pursuit signals loop through the cerebellum and on to the vestibular nuclei and the nucleus prepositus hypoglossi of the brainstem, which then passes on the final motor commands to the oculomotor muscles.

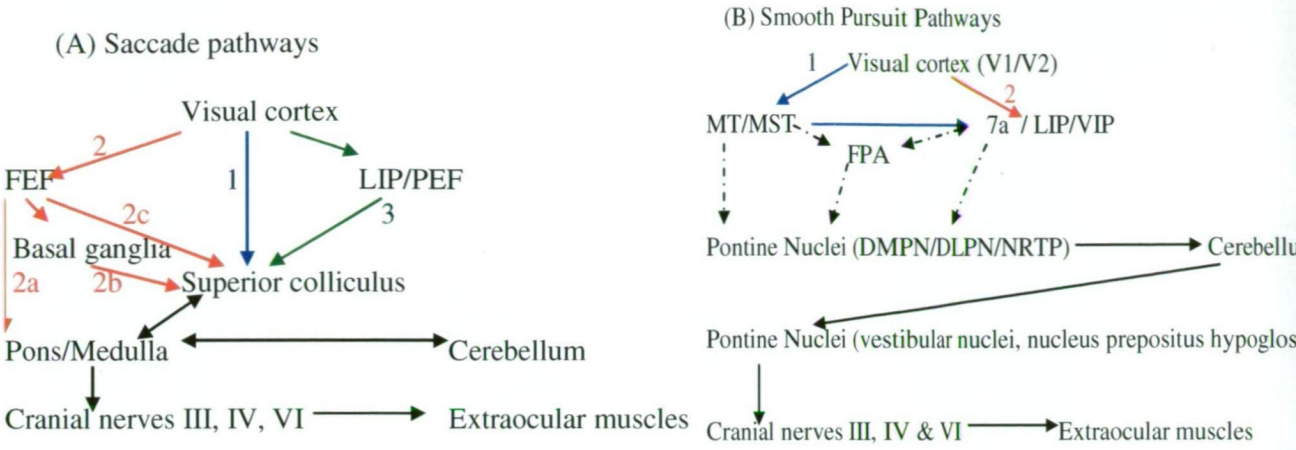

Figure 4. Diagram of the neurological pathways for (A) saccades and (B) smooth pursuit eye movements (dashed lines denote multiple possible connections).

Shared inputs and mechanisms for saccades and smooth pursuit

Evidence from a wealth of research on saccadic and pursuit eye movements over many years has led to the traditional view that the two eye movements represent different oculomotor systems, generated by largely distinct neuroanatomical pathways (Bach-y-Rita, 1973; Fuchs, 1967; Leigh & Zee, 1999; Lisberger et al., 1987; Rashbass, 1961). This is consistent with their distinct latencies, dynamics, and functions, as well as evidence from differential effects of lesions on saccades and pursuit, and recent neuroimaging evidence (Petit, Clark, Ingeholm, & Haxby, 1997; Rosano et al., 2002). Nevertheless, when reviewing the neural pathways involved in both types of eye movements, it is evident that they both involve complex networks of many similar structures (Krauzlis, 2004, 2005), often involving similar (Burke & Barnes, 2008) or distinct but adjoining regions of the same structures (O'Driscoll et al., 2000). Attempts to neatly assign discrete areas or pathways to the generation of either saccades or pursuit have been considered to be too simplistic (Krauzlis & Stone, 1999; Sharpe, 1998), because the two systems may not be completely independent. In this context, more recent research has focused on potentially shared

inputs and mechanisms of the saccadic and smooth pursuit systems, rather than focusing on their differences (Erkelens, 2006). This notion may help to explain how the two kinds of eye movements manage to collaborate so effectively during many everyday visual tasks, such as visual search or visual tracking (Krauzlis, Basso, & Wurtz, 1997).

In order to produce a saccadic and pursuit eye movement, many similar tasks are required (Kornyolo, Dill, Saenz, & Krauzlis, 2003), including the need to break from fixation, select a target, and execute the motor command. Early evidence that saccades and pursuit have shared inputs for selection and movement initiation were the findings that latencies in humans and monkeys for both types of eye movements display the same dependence on gap duration in a "gap paradigm" (Krauzlis & Miles, 1996a, 1996b, 1996c). Since then, a lot of evidence for shared inputs into saccadic and smooth pursuit eye movements has accumulated. For example, there are indications that saccades and pursuit share a common motor error that is based on position error which is considered to be encoded in the superior colliculus (Krauzlis et al., 1997). In addition, there is evidence for common mechanisms for visuo-spatial attention in both types of movement (S. A. Adler, Bala, & Krauzlis, 2002; Berman et al., 1999; Kimmig, Biscaldi, Mutter, Doerr, & Fischer, 2002; Krauzlis, Zivotofsky, & Miles, 1999; Madelain, Krauzlis, & Wallman, 2005). Finally, the two eye movements have been found to have shared inputs for target selection (Gardner & Lisberger, 2001; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003) and common inhibitory mechanisms regulating their initiation (Joiner & Shelhamer, 2006; Keller & Missal, 2003; Kornyolo et al., 2003; Missal & Keller, 2002; Ogawa & Fujita, 1998).

The above mentioned findings have been supported by related discoveries that neural substrates, which were previously thought to be exclusively associated with saccadic eye movements, also play a role in smooth pursuit. For example, the vermis of the cerebellum was traditionally believed to be involved only in saccadic eye movements, but it has now been implicated as a possible site of signal convergence for both saccades and pursuit (Krauzlis & Miles, 1998; Krauzlis & Stone, 1999). Similarly, there is considerable evidence that the superior colliculus, a structure historically assigned exclusively to saccades, is active during pursuit eye movements (Basso et al., 2000; Krauzlis, 2001; Krauzlis et al., 2000) and could be another site for signal convergence for both (Krauzlis et al., 1997; Krauzlis & Dill, 2002), influencing their target selection (Carello & Krauzlis, 2004). Furthermore, brainstem neurons have an established role in saccade generation, but in addition they have been found to be involved in pursuit generation, including burst neurons in the midbrain (Missal, De Brouwer, Lefèvre, & Olivier, 2000) and omnipause neurons in the pons (Keller & Missal, 2003; Missal & Keller, 2002). Such findings have contributed to the notion that the smooth pursuit and saccadic systems may be much more similar than previously thought (Berman et al., 1999; Krauzlis, 2004). Some neural structures may be more important in the generation of either type of ocular movement, but most structures are generally involved in the generation of both types of eye movements (Krauzlis & Stone, 1999) and a common neuro-anatomical pathway for saccades and pursuit has been proposed (see Figure 5). Hence, rather than viewing them as distinct eye movement systems with separate neuro-anatomical pathways, pursuit and saccadic eye movements have recently been conceptualised as different motor outcomes of a shared cascade of sensory-motor processes (Krauzlis, 2004, 2005; Krauzlis & Stone, 1999; Orban de Xifry & Lefèvre, 2007). The undisputed

differences in the dynamics and function of saccadic and pursuit eye movements are typically attributed to differences in their motor output pathways (Burke & Barnes, 2006; Joiner & Shelhamer, 2006; Kornyolo et al., 2003). Furthermore, it has been suggested that saccadic or smooth pursuit eye movements are selected based on different criteria, with pursuit having a lower threshold regarding its speed-accuracy trade-off (Krauzlis & Dill, 2002), a proposal that has received some support (Kornyolo et al., 2003; Liston & Krauzlis, 2005).

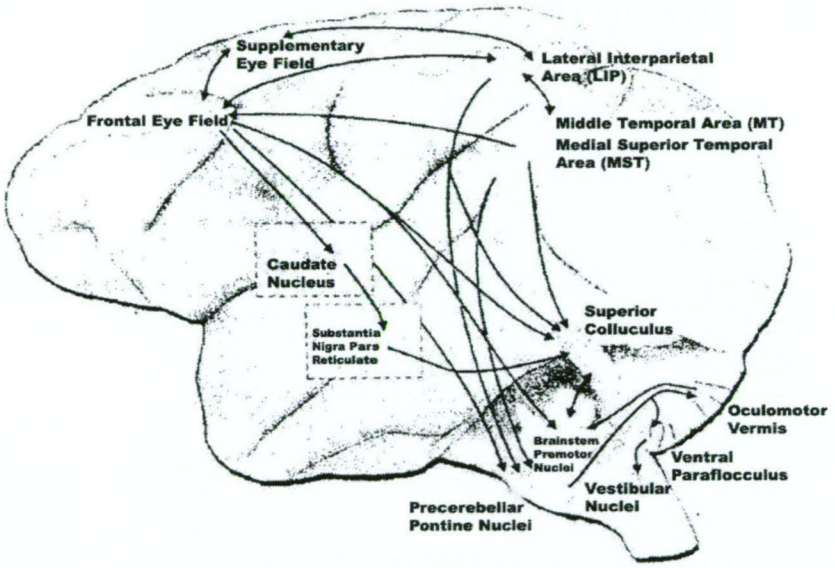

Figure 5. Common descending pathways for saccadic and pursuit eye movements on the lateral view of a monkey brain adapted from Krauzlis (2005, p.125). Arrows depict the (direct or indirect) anatomical connections between brain areas.

In summary, recent findings have challenged the complete independence of the saccadic and smooth pursuit eye movement systems and suggested that the two share some common inputs and mechanisms, particularly with regard to attentional mechanisms, target selection, and movement initiation. Furthermore, neural substrates typically only associated with saccades have been found to be involved in pursuit eye movements. The extent of the common inputs to saccadic and pursuit eye movements

and the degree of overlap in pathways has not yet been fully established, and views differ about whether saccadic and pursuit eye movements are two separate systems that are closely intertwined (De Brouwer, Missal, Barnes, & Lefèvre, 2002; Erkelens, 2006) or whether they represent two outcomes of one system (Krauzlis, 2004; Orban de Xifry & Lefèvre, 2007). Although this thesis does not directly investigate common inputs into the saccadic and smooth pursuit systems, it examines the close synergy between the two types of eye movements during visual tracking and seeks to discover how these eye movements work together when tracking a target by varying the parameters that may favour one kind of response over the other.

Chapter 4

Visual tracking

Saccadic and smooth pursuit components of visual tracking

Introduction

It was recognised very early (Dodge, 1903; Rashbass, 1961; Westheimer, 1954) that when observers visually track an object they do so using a combination of smooth pursuit and saccadic eye movements. Rashbass (1961) originally conceptualised saccadic and smooth components as two different ways of tracking a target, and he was interested in finding out what factors determine what strategy is chosen. However, despite this early recognition of these two aspects of visual tracking, for many years the term 'smooth pursuit' was used virtually synonymously with 'visual tracking'. Therefore, when pursuit was investigated, both saccadic and smooth components were generally included indiscriminately in the analyses, until Bahill, Iandolo, and Troost (1980) formalised the distinction and advocated separating out the two components, distinguishing between single and dual-mode pursuit. Since then, it is generally acknowledged that visual tracking consists of both smooth pursuit and saccadic eye movements (Becker, 1991; R. H. S. Carpenter, 1988; Hallett, 1986; Horii, 1994; Keller, 1991; Pola, 2002). Nevertheless, the removed saccades have been largely ignored in most studies until the late 1990s and only the smooth pursuit components were usually analysed. This limited interest in saccades during visual tracking reflects the traditional, very simple model of the interaction of smooth pursuit and saccadic eye movements in visual tracking: Smooth pursuit eye

movements are the main strategy used to track a target until the retinal position error caused by pursuit lag becomes large enough to trigger a corrective or 'catch-up' saccade (e.g., Ciuffreda & Tannen, 1995; Hallett, 1986; Lisberger et al., 1987). As the eye increasingly lags behind the target with increasing target velocity, there is a fairly linear relationship between the number of catch-up saccades and target velocity (Ciuffreda & Tannen, 1995; Collewijn & Tamminga, 1984; Eckmiller, 1987; Hallett, 1986; Lisberger et al., 1987; Pola, 2002; Westheimer, 1954). Also, there is a significant increase in the occurrence of large saccades at faster velocities (Schalen, 1980). While catch-up saccades are the main saccades that occur during pursuit, other saccade types have been identified, mainly intrusive saccades, such as anticipatory saccades and square-wave jerks (R. G. Ross, Olincy, Zerbe, & Radant, 2001; Shaffer, Krisky, & Sweeney, 2003). Unlike catch-up saccades, which bring the target closer to the fovea, intrusive saccades disrupt tracking by moving the eye away from the target, and they are more common in disordered tracking (R. G. Ross et al., 2001; White, St-cyr, Tomlinson, & Sharpe, 1983). However, others have conceptualised anticipatory saccades not as an intrusion, but as a functional and predictive part of visual tracking (Van Gelder, Andersen, Herman, Lebedev, & Tsui, 1990). Square-wave jerks are generally viewed as an intrusive saccade, followed by a contrary, corrective saccade and the rate of square-wave jerks decreases with increasing task demands, such as decreasing predictability of the target or increasing target velocity during visual tracking (Shaffer et al., 2003). Regardless of type of saccade, the saccadic component of visual tracking has only very recently been given proper attention, and both saccadic and smooth pursuit components and their interaction during visual tracking are finally being investigated. Concurrent investigations into potentially shared neural mechanisms of the two eye movements have also contributed to renewed interest in

this area, as there is some evidence that pursuit and saccades share target selection and movement initiation mechanisms (see Chapter 3).

Saccades during visual tracking

Whereas smooth pursuit eye movements mainly compensate for retinal velocity errors, saccades are generally believed to be triggered in response to a retinal position error (see Chapter 2). Examining saccades made during visual tracking shows that their main aim is to bring the target on or near the fovea by reducing the retinal position error. For saccades to stationary targets, position errors above 0.1-0.2 deg typically lead to a saccade, but during tracking, position errors up to several degrees can be tolerated (Eckmiller, 1987) depending on stimulus conditions. Target velocity is the main variable affecting saccades during tracking; at slow tracking velocities (up to 5.0 deg/s), small position errors of 0.2 deg/s elicit a corrective saccades, whereas at faster velocities larger position errors are required (Collewijn & Tamminga, 1984). At moderate to fast velocities, small position errors are generally tolerated without triggering a saccade (0.5 deg: Collewijn & Tamminga, 1984; 0.1-0.2 deg: Gellman & Carl, 1991) or causing a smooth pursuit response (Morris & Lisberger, 1987) and well practised observers can even purposefully suppress corrective saccades for position errors up to 2.5 deg (Puckett & Steinman, 1969). Not only are retinal position errors generally bigger for faster velocities, but saccade latency is shorter (Gellman & Carl, 1991), although this may be due to the fact that saccade latencies are generally shorter for saccades to large position errors (Becker, 1989; Blohm, Missal, & Lefèvre, 2004).

While saccades to moving targets are certainly triggered in part by position error, their long latency shows that they are planned quite some time before saccade onset. Yet, saccades are able to compensate for the ongoing motion of the target and to produce fairly accurate eye movements (e.g., Schreiber, Missal, & Lefèvre, 2006). This implies that saccades to moving targets must use additional information in their programming, but this issue has not yet been fully resolved (Eggert, Guan, Bayer, & Büttner, 2005). It has been suggested that some kind of prediction must be used by the system in addition to the retinal position error at time of saccade programming. In particular, it has been proposed that extrapolations based on target velocity information are used by the saccadic system to predict future target position (Fuchs, 1971; Rashbass, 1961; D. A. Robinson, 1965). This is consistent with lesion studies in monkey MT affecting only saccades to moving, but not stationary targets (Newsome et al., 1985), as MT provides information related to target motion. Early studies failed to find evidence to confirm this notion (Heywood & Churcher, 1981), at least not without extensive exposure to the target (Ron, Vieville, & Droulez, 1989a),but since then most studies have provided strong evidence for a role of target velocity in saccade generation to moving targets (Gellman & Carl, 1991; Keller & Johnsen, 1990; Kim, Thaker, Ross, & Medoff, 1997; Ron, Vieville, & Droulez, 1989b), although it is retinal slip velocity, rather than target velocity per se, that is used by the saccadic system (Blohm, Missal, & Lefèvre, 2003; De Brouwer, Missal et al., 2002; De Brouwer, Missal, & Lefèvre, 2001; De Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002; Guan, Eggert, Bayer, & Büttner, 2005; Schreiber et al., 2006). Because velocity extrapolation is better once pursuit is engaged and the system has been exposed to the motion, this effect is stronger during maintained pursuit than during initiation (Kim et al., 1997). The above mentioned studies all used horizontal

tracking, but an effect of target velocity on saccade programming has also been found for two-dimensional target motion (Engel, Anderson, & Soechting, 1999; Schreiber et al., 2006). Hence, current evidence generally indicates that both retinal position error and retinal slip velocity are used by the saccadic system to program saccades to moving targets, with retinal slip velocity being integrated over the period of saccade latency and saccade duration (De Brouwer, Missal et al., 2002). These signals are viewed as quite independent from one another (Schreiber et al., 2006) and are know to use separate neural pathways (Keller, Gandhi, & Weir, 1996). In terms of underlying mechanisms, it has been suggested that the cerebellum is the main neuroanatomical site for velocity extrapolation for saccade programming (Guan et al., 2005; Optican & Quaia, 2002).

Saccades made in response to stationary and moving targets are believed to have the same underlying initiation mechanism for triggering the saccade (Krauzlis & Miles, 1996b). Nevertheless, saccades to stationary and moving targets have repeatedly been found to vary in their dynamics and main sequence (Blohm et al., 2003; De Brouwer, Missal et al., 2002; De Brouwer et al., 2001; Eggert et al., 2005; Keller et al., 1996), with different amplitude, peak velocity, and duration. Furthermore, when comparing saccades made in the same direction as pursuit (*forward* saccades) with those made in the opposite direction of pursuit (*backward saccades*), they also vary in their dynamics and main sequence, with forward saccades having shorter latencies (Smeets & Bekkering, 2000; Tanaka, Yoshida, & Fukushima, 1998), larger amplitude (De Brouwer, Missal et al., 2002), and longer duration and lower peak velocity (Eggert et al., 2005; Guan et al., 2005) than backward saccades. Saccades to stationary targets generally have parameter values in between forward and backward saccades.

Interestingly, when the pursuit component was removed from the saccades, De Brouwer, Missal, Barnes, and Lefèvre, (2002) found that the difference between stationary, forward and backward saccades was no longer significant, and they recommend always correcting saccade characteristics for pursuit velocity. This indicates that the differences that were previously found between the dynamics of saccades to stationary and moving targets do not reflect differences in underlying saccade mechanisms, but simply suggest that for moving targets a smooth pursuit velocity component is added to the saccades. Indeed, there is evidence that the mechanisms underlying saccadic eye movements in response to moving stimuli are very similar to those to stationary stimuli (Kimmig et al., 2002).

Effects of saccades on smooth pursuit

Not only are saccades during visual tracking affected by the smooth pursuit response, but there is also evidence that pursuit eye movements are in turn affected by saccades. Presaccadic pursuit acceleration is generally less than 50deg/s^2 (Carl & Gellman, 1987), depending on target velocity, and pursuit velocity is dependent on the latency of the initial saccade (Ogawa & Fujita, 1998). Furthermore, pursuit eye velocity is strongly enhanced immediately after a saccade, both in the same and opposite direction of pursuit (Gardner & Lisberger, 2001; Lisberger, 1998; Schoppik & Lisberger, 2006), as is pursuit acceleration (Ogawa & Fujita, 1998). Such *postsaccadic enhancement* had previously been found in ocular following (eye movement evoked by motion of a larger visual field) (Kawano & Miles, 1986) and disparity vergence (Busettini, Miles, & Krauzlis, 1996). In those cases postsaccadic enhancement was attributed to the image acceleration during the saccade. However, Lisberger suggested that during foveal pursuit postsaccadic enhancement is caused by

a spatially selective, cognitive control mechanism related to the saccade itself. Target motion is processed preferentially at the endpoint of the saccade, because the selected target is about to be brought closer to the fovea (Gardner & Lisberger, 2001; Lisberger, 1998; Schoppik & Lisberger, 2006). Another explanation is that postsaccadic pursuit enhancement is the result of generally increased motion sensitivity immediately after a saccade (Ibbotson et al., 2007; Reppas et al., 2002) because of previously suppressed visual motion processing during the saccade (see Chapter 2). Hence motion processing is briefly enhanced immediately after the saccade, possibly to compensate for the preceding magnocellular suppression. However, other studies have found that motion perception was negatively affected by saccades (C. Lee & J. Lee, 2005), showing a motion processing bias in the direction opposite to the saccade, both before (J. Lee & C. Lee, 2005) and up to 100ms after a saccade (Park, Lee, & Lee, 2001). Furthermore, there is some evidence that this postsaccadic enhancement is only present in corrective catch-up saccades, which bring the target closer to the fovea. There is some evidence that for anticipatory saccades (and even 3-12% of catch-up saccades), there is actually an opposite effect; postsaccadic slowing (R. G. Ross et al., 2001). The authors suggested that this is due to anticipatory saccades generally overshooting the target, and therefore letting it 'catch-up'. This is consistent with Lisberger's explanation of postsaccadic enhancement (Gardner & Lisberger, 2001; Lisberger, 1998), proposing that smooth pursuit is only enhanced when the saccade results in bringing the target closer to the fovea.

The coordination of saccades and smooth pursuit during visual tracking

Saccadic and pursuit eye movements mutually affect one another and there is evidence for a motion velocity input into saccadic eye movements (e.g., De Brouwer, Missal et al., 2002; De Brouwer et al., 2001) and a position input into smooth pursuit eye movements (e.g., Blohm, Missal, & Lefèvre, 2005; Morris & Lisberger, 1987), as summarised comprehensively by Orban de Xifry and Lefèvre (2007). There is also accumulating evidence of shared inputs and mechanisms of the two systems, although it is not yet established whether the two represent separate systems, which are closely intertwined, or two outcomes of a single system (see Chapter 3; Krauzlis, 2004; Krauzlis, 2005). While we are not yet able to fully understand the synergy of saccades and pursuit during visual tracking, more attention has been given to this question in recent years, and some advances have been made in our understanding of this matter.

Rashbass (1961) originally concluded that visual tracking consisted of "the superimposed movements of two independent systems" (p.335) fulfilling different demands, although he later (1971) asserted a stronger interaction between the two. As previously discussed, the traditional model was very simple: pursuit eye movements respond to retinal motion, while catch-up saccades correct for position error, typically when the eye lags behind at moderate to fast velocities (Ciuffreda & Tannen, 1995; Eckmiller, 1987; Hallett, 1986; Lisberger et al., 1987; Pola, 2002; Westheimer, 1954). Conceptualised more broadly, Collewjin and Tamminga (1984) suggested that smooth pursuit is generally the weaker or more vulnerable tracking component and that the relative contribution of saccadic eye movements increases whenever the tracking task becomes more difficult, with increases in velocity being one example of

that. Nevertheless, the two components of eye tracking were conceptualised as completely separate and a linear addition of the two was ruled out (Jürgens & Becker, 1974). Despite this view, some researchers have removed the pursuit components from the saccades (Keller & Johnsen, 1990; Smeets & Bekkering, 2000), assuming there was a pursuit effect on saccadic eye movements. De Brouwer, Missal, Barnes, and Lefèvre (2002) clearly demonstrated the addition of the pursuit component to the saccades made during tracking and offered a simple correction to apply to saccade amplitude and saccade peak velocity when examining such saccades, and this correction has since been adopted in other studies (Blohm et al., 2003; Blohm et al., 2004; Eggert et al., 2005; Guan et al., 2005). This is consistent with the *superposition* hypothesis, asserting that the main sequence of saccades and pursuit are linearly added for saccades during visual tracking, while the pure saccade dynamics are similar for saccadic eye movements made to stationary and moving stimuli.

With regard to more detailed modelling of the synergy of saccadic and smooth pursuit components of visual tracking, both position error and retinal slip signals need to be considered. Gardner and Lisberger (2001) suggested that because both tracking components use both position and velocity information, coordination of the two eye movements occurs at the level of target selection. Erkelens (2006) also proposed that the coordination of the two eye movements occurs at the level of target selection, in addition to shared attentional processes. Lisberger and colleagues suggested a sequential model of shared target selection (Gardner & Lisberger, 2001, 2002; Schoppik & Lisberger, 2006), while Krauzlis and colleagues suggested a parallel model (Krauzlis, 2004, 2005; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003, 2005). Current evidence tends to support the a parallel model of target selection (Case &

Ferrera, 2007). In relation to what triggers a saccade during ongoing tracking, De Brouwer, Yuksel, Blohm, Missal, and Lefèvre (2002) proposed a model for saccade generation in visual tracking, with *eye crossing time* as the main factor in determining whether a saccade is initiated. Eye crossing time is the time necessary for the eye to cross the target at constant eye velocity and it in turn depends on position-error and retinal slip (position error divided by retinal slip). If eye crossing time enters the *saccadic zone* (below 40ms or above 180ms), it is unlikely to catch the target solely by means of a smooth acceleration, and a catch-up saccade is triggered. This model of saccade generation during tracking was adopted by Orban de Xifry and Lefèvre (2007) in their model of visual tracking.

In the absence of retinal inputs (e.g., tracking in the dark), extraretinal inputs are not only used by the pursuit system to continue tracking (Becker & Fuchs, 1985; Bennett & Barnes, 2003), but also by the saccadic system and to coordinate saccadic and pursuit components, although with a 400ms time delay (Blohm et al., 2003; Blohm et al., 2004). Similarly, during transient target disappearance, the saccadic system uses extraretinal information, based on efference copies of retinal slip and position errors (Orban de Xifry & Lefèvre, 2007), to supplement the ongoing but decaying smooth pursuit with corrective saccades (Bennett & Barnes, 2006). In doing so, saccades and smooth pursuit work in synergy, with the saccadic component adjusting its input depending on the pursuit's contribution (Orban de Xifry, Bennett, Lefèvre, & Barnes, 2006). Blohm, Optican, and Lefèvre (2006) have proposed a formal model of how efferent smooth eye velocity commands could be used to coordinate saccadic and smooth eye movement during tracking in the absence of retinal inputs. This model involves slow, delayed integration of the smooth eye velocity signals, and the

simulations of their model are promising. The current thesis aims to further investigate the synergy of saccadic and smooth pursuit eye movements in the visual tracking of a target, with continuous and apparent motion visual inputs.

Visual tracking of apparent motion

Introduction

Apparent motion (also called 'discrete', 'discontinuous' or 'sampled' motion) refers to motion in the absence of real or continuous motion. This can be produced by a stationary stimulus presented in succession or a moving stimulus, which is only illuminated intermittently or is regularly occluded. The fact that two discrete stimuli can, under the right conditions, elicit the perception of continuous motion was first discovered by Exner (1875) and became an important paradigm in studying motion perception mechanisms (see Chapter 5). Initially there was some doubt whether the perception of real and apparent motion are governed by the same mechanisms because they can exhibit some phenomenological differences (Anstis, 1978; M. Green & Von Grunau, 1983; Kolers, 1972, 1983). In particular, as apparent motion can be perceived at higher velocities than continuous motion under the same viewing conditions it was hypothesised that apparent motion may serve the function of extending the velocity range of motion perception (L. Kaufman, Cyrulnick, Kaplowitz, Melnick, & Stof, 1971). However, the dominant view today is that continuous and apparent motion are generated by the same underlying mechanism (Anstis, 1986; Braddick, 1980; Burr, 1991; Gregory & Harris, 1984; Kaneoke, Bundou, Koyama, Suzuki, & Kakigi, 1997; Larsen, Madsen, Lund, & Bundesen, 2006; Purves, Paydarfar, & Andrews, 1996). Breaking up the continuous motion

signal into its spatial and temporal components is viewed as a valid and necessary way to investigate motion perception mechanisms (Braddick, 1980; Grossberg & Rudd, 1992; Zhuo et al., 2003), processes in visual (M. M. Churchland & Lisberger, 2000) and attentive tracking (Shioiri, Cavanagh, Miyamoto, & Yaguchi, 2000; Verstraten, Cavanagh, & Labianca, 2000), as well as shared mechanisms underlying perception and pursuit (A. K. Churchland, Huang, & Lisberger, 2007; A. K. Churchland & Lisberger, 2001; Madelain & Krauzlis, 2004).

Apparent motion as a stimulus for visual tracking

Apparent motion paradigms have been used extensively to investigate motion perception, but it has not yet been used as widely in the study of eye movements. At first, it was generally believed that a continuously moving stimulus was necessary to elicit smooth pursuit eye movements (e.g., Kowler, 1990), even though it had been demonstrated that similar eye movements could be elicited by intermittently illuminated stimuli (e.g., Hansel, 1953). More specifically, Westheimer (1954) showed that intermittently exposed moving stimuli (stimulus duration of 10ms and interstimulus intervals of 120 or 240ms) gave rise to smooth pursuit eye movements very similar to those observed with continuous motion, although with lower gain and more frequent saccades. Steinbach (1976) demonstrated that illusionary targets were able to elicit pursuit eye movements and Stoper (1967, cited in Bridgeman, Mayer, & Glenn, 1976) used stroboscopically illuminated stationary targets ("picket-fence illusion") to elicit smooth tracking. Lamontagne (1973) then formally presented the use of this specific kind of apparent motion (later called *sigma movement*, Behrens & Grüsser, 1979) as an experimental paradigm in the study of eye movements and motion perception. In this paradigm the eye movement is initiated by a real moving

target and the perceived ongoing target motion is dependent on the pursuit eye movement itself. Lamontagne outlined theoretically how target velocity, stimulus duration, and interstimulus distance are interrelated and he suggested a number of variations of the paradigm and their potential use. Heywood (1973) then experimentally applied this paradigm, systematically varying spatial separation, flash rate and therefore target velocity. He demonstrated that very good smooth pursuit eye movements were elicited by stationary dots and that smooth pursuit was negatively affected by increasing the spatial separation and the flash rate. The frequency and size of saccades was also affected by these variables, with generally larger and more frequent saccades associated with larger spatial separations and faster flash rates. Behrens and Grüsser (1979) demonstrated that that smooth eye velocity and perceived velocity of sigma motion depended on flash duration and flash frequency. They proposed that eye velocity is the product of a constant k (usually 1, exceptionally 2 or 3), the stimulus duration, and the stimulus frequency ($V_e=k * P_s * f_s$). It was later found that *k* can range from 1 to 7 (Lamontagne, Gosslin, & Pivik, 2002), suggesting that sigma pursuit can be evoked at much faster velocities than originally thought. When tracking of continuous and apparent motion were compared directly, it was found that smooth pursuit was as good, or better, in response to apparent motion, with higher gain and less frequent saccades (Fetter & Buettner, 1990; Van der Steen, Tamminga, & Collewijn, 1983). Sigma-motion and the resulting sigma-optokinetic eye movements became a popular tool for studying eye movements (D. Adler et al., 1981) and it has since been used in numerous studies to investigate, in particular, the optokinetic system (e.g., D. Adler & Grüsser, 1982; Flandrin, Courjon, Magnin, & Arzi, 1990; Tong, Peng, & Sun, 2003).

With regard to apparent motion, using actual discrete target displacements (also called *beta movement*, Wertheimer, 1912), Morgan and Turnbull (1978) were one of the first to systematically investigate the tracking using intermittently illuminated stationary targets. They found that smooth pursuit became increasingly interrupted by saccades when the temporal separation of targets exceeded 150ms, but some smooth pursuit was generated with temporal separations as large as 300ms. Similar pursuit deficits at temporal separation of 80-100ms were obtained in other studies (e.g., Fetter & Buettner, 1990; Van der Steen et al., 1983). However, these studies generally used only slow to moderate target velocities (M. M. Churchland & Lisberger, 2000). Barnes, Donnelly, and Eason (1987) also examined pursuit in response to intermittently illuminated stationary targets, but the authors varied stimulus duration of the stationary targets (from 10-320ms). They found that increasing stimulus duration resulted in a significant decrease in eye velocity, as would be expected, as the pursuit system receives zero-velocity feedback during target presentation. They also found evidence for predictive pursuit, as eye velocity increased before target appearance and then decreased when the target was extinct.

Barnes and Asselman (1992) systematically investigated intermittently illuminated moving targets at varying pulse durations and temporal separations in humans. They demonstrated that eye velocity was modulated in a pulsatile manner especially when temporal separation exceeded 1,000ms. In these conditions eye velocity increased with each target presentation and then decreased exponentially during the subsequent target disappearance, consistent with research on transient target disappearance during ongoing pursuit (e.g., Becker & Fuchs, 1985; Madelain & Krauzlis, 2003). At temporal separations below 1,000ms there was a summation of the transient responses of each target presentation, resulting in very smooth tracking at temporal separations

as low as 320ms. They also found evidence of prediction; after only a few target presentations eye velocity increased 200-300ms prior to target appearance, and therefore well before visual feedback became available (100ms latency). In a similarly systematic study Churchland and Lisberger (2000) used intermittently illuminated stationary flashes to investigate the spatial and temporal limits of smooth pursuit during both pursuit initiation and maintenance in monkeys. They demonstrated that pursuit has both temporal and spatial limits, depending on target velocity. They concluded that during pursuit initiation, pursuit deficits with apparent motion stimuli were due to failures of the visuo-motor drive to fully support eye acceleration, as evidenced by longer eye acceleration latencies and slower peak acceleration. During maintenance, pursuit deficits consisted of lower gain and were explained by failure of the eye velocity memory due to the apparent motion signal being not sufficient to fully engage the pursuit system. Unfortunately, they did not investigate the saccadic contribution of the visual tracking response and excluded trials with excessive saccades.

The use of apparent motion has since also been applied to disordered visual tracking in a large number of observers with schizophrenia and controls (Slaghuis, Hawkes, Holthouse, & Bruno, 2007a), using intermittently illuminated stationary targets (*jumping-dot* paradigm). They tested a range of velocities (5.0-35.0deg/s), varying temporal separation of the targets. Smooth pursuit was generally better for continuous than jumping-dot motion and this difference became larger with increasing target velocity. When continuous motion was used, smooth pursuit of observers with schizophrenia and controls only differed in their single-mode gain at very fast velocities (≥20.0deg/s), as found in previous research (Clementz & McDowell, 1994;

Thaker, Ross, Buchanan, Adami, & Medoff, 1999). Interestingly, with jumping-dot motion, the tracking deficit in schizophrenia was evident for all slower velocities, and a significantly greater proportion of observers with schizophrenia exhibited a visual tracking deficit compared to controls in response to jumping dot than continuous motions. The authors also examined the saccadic contribution to visual tracking and found no significant difference in saccade frequency or saccade characteristics between continuous and jumping-dot motion. Another very interesting finding was that by degrading the motion signal disordered tracking could be evoked in normal observers, which resembled visual tracking in schizophrenia, with decreased gain and increased saccade frequency. These findings suggest a great potential of apparent motion paradigms in the study of visual tracking.

In summary, previous research using apparent motion stimuli to investigate both normal and disordered visual tracking have resulted in very interesting findings, which demonstrate that these stimuli give the researcher greater control in terms of what signals are provided, not only in terms of their spatial and temporal parameters, but also concerning the extent of exposure to those signals. These paradigms therefore have the potential to reveal underlying mechanisms in normal observers, as well as the underlying deficits in disordered tracking. Paradigms that have been used previously vary regarding whether the stimulus contains position information only (intermittently illuminated stationary targets) or position as well as motion information, with regard to position and velocity (intermittently illuminated moving targets), but the two paradigms have never been directly compared under the same conditions. Previous studies have used a narrow range of velocities and have never examined velocities slower than 2.0 deg/s. In addition, only the effects of apparent

motion on smooth pursuit tracking have been examined and have almost entirely ignored the saccadic components of visual tracking. One of the aims of this thesis is to examine the role of saccadic and smooth pursuit components of visual tracking using apparent motion paradigms. In particular, the use of apparent motion stimuli aims to separate spatial and temporal parameters as well as stimulus position and velocity inputs for visual tracking.

Chapter 5

The visual perception of motion

Motion perception and its thresholds

Introduction

Motion is the result of a change in position over time (e.g., Sekuler et al., 1990) and motion perception is the detection and integration of these spatial changes of an image across the retina over time (e.g., Snowden & Braddick, 1989a). The perception of visual motion therefore involves the study of all aspects of the detection and encoding of the moving image across the retina of the eye, and is an operation that is performed locally and in parallel for all points in the image, and all subsequent computations are based on the local retinocentric measurements (Smith & Snowden, 1994). Such motion across the retina can be produced in a number of ways, and can include observer motion, autokinetic motion, motion aftereffects, induced motion, as well as actual object motion and apparent motion (Wade & Swanston, 1991). Observer motion relates to motion of an image over the retina that results from a change of the position of the eye in space (e.g., eye/head movements, body movements etc.). Autokinetic movement (or autokinesis) refers to the phenomenon of random motion of a speck of light in a dark environment, such as an isolated star in the sky. This is generally thought to be a consequence of fixational eye movements and imperfect image stabilisation (see Riedel et al., 2005) that the visual system cannot compensate for in the absence of any visible frame of reference. Motion aftereffects describe a whole range of illusions of motion in one direction after

adaptation to a motion stimulus in the opposite direction, such as seeing stationary rocks move upwards after watching a waterfall for a period of time (hence it is sometimes called the *waterfall illusion*). Motion of an object can also be induced by movements of the background and/or adjacent objects. Actual object motion refers to real motion of an object or pattern in space producing continuous motion of the corresponding image across the retina. Apparent motion on the other hand refers to the perception of motion in the absence of real motion, such as produced by a stationary stimulus presented in succession or an intermittently occluded moving stimulus (see Chapter 4).

Apart from the different ways in which motion over the retina can be produced, there are also various distinctions in regards to the type of motion involved. One way of categorizing motion is using the local versus global dichotomy (Born & Tootell, 1992; Julesz, 1971). Local motion refers to a single object or a small group of objects moving in a specific location of the visual field. Global motion on the other hand refers to a global perception of motion across a larger area of the visual field, and this motion can be made up of a proportion of individual objects all moving coherently in one direction, such as in a random dot kinematogram (also called *coherent motion*). Another way to classify motion is to distinguish between short-range and long-range motion (Braddick, 1974, 1980). These were believed to be governed by distinct mechanisms, with short-range motion processed by low-level detectors and long-range motion being governed by higher-level cognitive processes. However, this dichotomy has now largely been replaced by the more recent distinction between first- and second-order motion (Cavanagh & Mather, 1990; Chubb & Sperling, 1988). First-order motion is defined by spatiotemporal changes in luminance, while second-

order stimuli involve more complex percepts evoked by spatiotemporal changes in depth, contrast, or texture. A third, attentional mechanism has also been proposed, adding a more active top-down process to motion perception (Horowitz & Treisman, 1994; Lu & Sperling, 1995a, 1995b). The present chapter outlines the parameters of motion perception, as well as the models and neurology of motion perception and how these relate to saccadic and smooth pursuit eye movements.

Factors affecting motion perception

In investigating the perception of motion, various different measurement paradigms and motion displays have been used. Both continuous and apparent motion stimuli are often employed and the stimuli can be presented in a number of ways. Bonnet (1980) defines the more classic motion displays, such as oscillatory motion displays (repetitive alternating two motion translations in opposite directions) being either sinusoidal (changes in velocity over time) or triangular (constant velocity), as well as frequency motion displays (such as spatial frequency drifting gratings). Oscillatory motion is usually defined by the direction of motion and its velocity, while a frequency motion display is mainly defined by the spatial and temporal frequency of the grating stimuli. With the advances in both theory of motion perception and available technology over the past 20 years the number of available motion displays has increased enormously and includes numerous continuous and apparent motion displays for both first- and second-order motion. One technique that is frequently used to study mechanisms underlying motion perception uses motion adaptation. Adaptation to motion occurs after prolonged exposure to a motion stimulus and decreases subsequent sensitivity to motion using the same mechanisms. If motion sensitivity to a subsequent stimulus is not decreased by adaptation, it can be

concluded that different mechanisms are involved in its processing. However, investigating motion perception commonly involves examining motion sensitivity; the ability of the motion system to detect motion. It is typically expressed in terms of a motion threshold; the minimum or maximum value for the detection of motion in terms of one limiting stimulus variable (Bonnet, 1980). Usually, the criterion for motion sensitivity is detection of the *direction* of motion (Bonnet, 1980; Burr & Ross, 1982) even though the thresholds for detection of the stimulus and identification of its direction are often similar for achromatic motion (Dobkins & Albright, 1998; Smith, 1994b). Another measure that is sometimes used in motion perception research is velocity discrimination, and experiments using this measure test the ability of observers to judge differences between speeds, and motion sensitivity is usually expressed as a Weber fraction ($\Delta V/V$). Weber fraction values between 0.06 and 0.08 are typically reported for velocities between 4.0-64.0 deg/s (see McKee & Watamaniuk, 1994), but because many other variables covary with target velocity, such speed discrimination experiments can be, according to some, 'a methodological nightmare' (McKee & Watamaniuk, p.103).

Motion sensitivity is affected by a large number of factors (Henderson, 1971), including stimulus velocity, amplitude (distance travelled), duration, luminance level, size and spatial frequency of the stimulus, contrast, and retinal eccentricity (Bonnet, 1980; Graham, 1965). The effects of these variables on motion sensitivity are usually curvilinear and the influencing variables interact strongly with one another (Bonnet, 1980). The most complex relationship, however, is between target velocity and motion sensitivity. Generally, the effects of velocity follow an inverted U-shape pattern (Lankheet, Van Doorn, Bouman, & Van de Grind, 2000), with lower motion

sensitivity at very high and low velocities. The optimal velocity depends largely on the spatial frequency of the target (Burr & Ross, 1982; Watanabe, Mori, Nagata, & Hiwatashi, 1968). In addition, there is evidence suggesting that motion detection is qualitatively quite different for slow and medium-to-fast target velocities (Henderson, 1971). Similarly, the effects of amplitude and duration of the movement on motion sensitivity have been found to be curvilinear with the optimal value depending on other variables (Bonnet, 1980; Post, Scobey, & Johnson, 1984). For example, the effects of amplitude depend on target velocity, with amplitude being a more important factor at low velocities (Bonnet, 1980). In regards to duration, for unidirectional movements, low durations decrease sensitivity, while for oscillatory movements duration does not affect sensitivity (Post et al., 1984). The effect of stimulus size on motion sensitivity is not straight forward either (Bonnet, 1980) and appears to also depend on target velocity. At very slow velocities, smaller stimulus sizes tend to give better motion sensitivity, while at fast velocities, larger stimulus sizes are associated with better motion sensitivity. Bonnet relates this to the spatial frequencies associated with different target sizes, and indeed the spatial frequency of the target is a crucial factor for motion sensitivity and optimal target velocity (Burr, 1991; Burr & Ross, 1982). On the other hand though, larger objects tend to appear to move slower than smaller objects (Brown, 1930), which renders this relationship even more complex. With regard to luminance levels, early research reported that at low luminance levels motion sensitivity increases very rapidly with increasing luminance, and then more slowly at higher luminance level until a maximum luminance value is reached (Brown, 1930; Graham, 1965). However, more recent studies have found that under general viewing conditions motion sensitivity is largely unaffected by luminance to levels as low as 0.05 cd/m^2 (Henderson, 1971; Lankheet et al., 2000).

The effects of retinal eccentricity of the target on motion sensitivity similarly depend on the other variables (Bonnet, 1980). The general trend is a linear decrease in motion sensitivity with increasing eccentricity (Graham, 1965; McKee & Nakayama, 1984; Post et al., 1984), and this decline is much more pronounced for slower target velocities (McKee & Watamaniuk, 1994). Also, while the direction of motion does not affect motion sensitivity in central vision, in the periphery motion sensitivity can vary depending on the direction of motion (Raymond, 1994). Although peripheral vision has often been said to be specialized for motion detection (Bonnet, 1980), this is not technically true (McKee & Nakayama, 1984), as the fovea has better absolute motion sensitivity than the periphery. However, motion sensitivity decreases only slightly with increasing eccentricity and to a much lesser extent than visual acuity decreases with eccentricity (Bonnet, 1980). In contrast, temporal sensitivity (velocity discrimination) has been found to be similar across the visual field (McKee & Nakayama, 1984). This suggests that even though absolute motion sensitivity is better in central vision, the periphery is more specialized for the detection of motion than for most other visual tasks.

Stimulus contrast also markedly affects motion perception. Motion sensitivity thresholds increase with decreasing contrast at very low contrast levels (below 0.05 log contrast) but are unaffected at higher contrast levels (Johnston & Wright, 1985), at least when frequency motion displays are used. For edge targets there is a much stronger contrast effect with motion sensitivity improving significantly with increased contrast (McKee & Watamaniuk, 1994). Edwards, Badcock, and Nishida (1996) found that the effects of contrast on motion sensitivity were different for local and

global motion. Furthermore, contrast has been found to affect perceived velocity (Johnston & Wright, 1985; Stone & Thompson, 1992; Thompson, 1982), and this effect is different at slow and fast velocities (Blakemore & Snowden, 1999; Thompson, 1982), with a reduction in contrast decreasing perceived velocity at slow target speeds, and increasing perceived velocity at fast target speeds (Thompson, 1982). Because many of the previously mentioned variables that affect motion perception also affect the perceived velocity of a target (Brown, 1930), it is therefore likely that many variables, which affect motion sensitivity, also have indirect effects mediated by perceived target velocity.

The visual system's sensitivity to motion can be expressed using different types of motion thresholds. The most commonly reported motion threshold is the *lower* motion threshold, the smallest value of a stimulus variable necessary for the detection of motion. Other thresholds are the optimal values for motion perception, as well as the *upper* motion threshold or *fusion* threshold, which occurs when the percept is no longer that of a moving stimulus but a line filling the entire trajectory of the movement (Bonnet, 1980; Brown, 1930). These motion thresholds can be expressed in regards to different limiting variables, including spatial displacement, target velocity and – most commonly- contrast/modulation. As previously outlined, motion thresholds can vary significantly depending on the stimulus characteristics and testing conditions and it has therefore been argued that motion threshold values are only valid for the context in which they were obtained (Johansson, 1978). For example, depending on velocity, movements across spatial displacements of less than 10 arc seconds can be detected when the moving stimulus is near a stationary reference (relative motion threshold). However, absolute motion thresholds (no stationary

reference) are much higher (Graham, 1965); at least in central vision (McKee & Watamaniuk, 1994). Also, at high contrast, lower limits of 1 deg/s can be perceived in central vision, while velocities as high as 10-20 deg/s are necessary for motion detection in the periphery (Johansson, 1978). Under optimal conditions, the lowest velocity at which motion can be perceived was found to be 0.02 deg/s (Smith, 1991), although there is some evidence that at slow velocities the crucial factor is not the velocity itself, but the overall spatial displacement (Boulten, 1987, cited in Smith, 1991). The fusion threshold of motion perception in terms of velocity was traditionally reported to be at 100 deg/s (see Burr, 1991). However, this upper limit depends on other factors, such as spatial frequency of the stimulus. For example, Burr and Ross (1982) showed that motion at velocities as high as 10,000 deg/s could be perceived for a very low spatial frequency stimulus (a 80.0 deg bar). Motion perception therefore appears not limited by an absolute threshold of any variable, but by the combination of all the variables, probably relating to the temporal resolution of the visual system (Burr, 1991).

The most common way of measuring and expressing motion sensitivity is contrast, the ratio of target intensity to background intensity (Watson, 1986). The motion contrast sensitivity threshold is the lowest contrast at which motion can be perceived and plotting contrast sensitivity versus another parameter (such as spatial or temporal frequency of the target) gives the contrast sensitivity function. Traditionally, contrast sensitivity measures were obtained using spatial gratings of various spatial frequencies (in cycles per degree- c/deg) and flickering or drifting at various temporal frequencies (in Hertz- Hz) (Kelly, 1977). The spatial contrast sensitivity function of stationary targets is generally bandpass with peak sensitivity around 5-6 c/deg spatial

frequency (peak sensitivity shifts downwards with decreasing luminance levels). Temporal contrast sensitivity functions have a similar shape with a sharp decline in sensitivity at high frequencies and a slower decrease at the low frequency end. However, the spatial and temporal parameters are not independent of one another, and the spatial contrast sensitivity function depends on the temporal frequency of the target and vice versa. At high temporal frequencies, the peak sensitivity shifts downwards to lower spatial frequencies and the low frequency attenuation disappears, rendering the contrast sensitivity function lowpass (see R. L. De Valois & De Valois, 1988). When temporal frequency is expressed as target velocity of the moving stimulus (deg/s) and measured for a range of spatial frequency targets (gratings as well as objects), individual bandpass contrast sensitivity functions are obtained for each velocity. Each function peaks at a different spatial frequency, with peak sensitivity occurring at higher spatial frequencies with faster target velocities (Burr & Ross, 1982; Kelly, 1979). In other words, the lower the spatial frequency of the target stimulus, the higher the optimal target velocity for peak sensitivity.

Whereas most research on motion sensitivity has studied first-order motion, in recent years motion sensitivity to second-order motion has also been investigated. Results indicate that the visual system is much more sensitive to first- than to second-order motion (Allard & Faubert, 2007; Hutchinson & Ledgeway, 2006; Schofield & Georgeson, 2003; Smith & Ledgeway, 1998). There are also some qualitative differences in motion sensitivity to the two types of motion. For example, increasing target velocity improves detection of first- but not second-order motion (Smith, 1994b), and the respective temporal contrast sensitivity functions differ significantly (Hutchinson & Ledgeway, 2006; Smith & Ledgeway, 1998). When recorded under

the same testing conditions, first-order motion contrast sensitivity is generally bandpass, peaking at medium drift velocities. Second-order motion sensitivity functions on the other hand peak at much slower velocities and then decline rapidly with increasing velocity, following a low-pass pattern. Both types of motion are similarly affected by eccentricity (Smith & Ledgeway, 1998; Solomon & Sperling, 1995), although there is some evidence that second-order motion sensitivity declines more rapidly in the periphery (Smith, 1994b).

In summary, there are many ways in which motion sensitivity can be expressed and there are numerous factors that affect the absolute motion threshold values. Motion sensitivity thresholds should therefore always be interpreted in the context of their testing conditions (Johansson, 1978). It has also been suggested that ideally, the study of motion perception should include a large number of paradigms, measuring responses in various locations of the visual fields and across a wide range of target velocities (Sekuler, Ball, Tynan, & Machamer, 1980).

Motion mechanisms and models of motion perception

Introduction

A crucial milestone in motion perception research was the work of Exner (1875), who showed that motion could be perceived by the visual system from stationary images presented in succession (Smith & Snowden, 1994). While this phenomenon had been known for some time, Exner elicited it with stimuli so close together in space that they could not be distinguished, implying that motion perception was not inferred from other information but must be a distinct and separate sensation. Nevertheless,

the question whether motion is a basic phenomenological dimension (like e.g., colour) or is derived from more basic sensory processes (such as space and time) still remains open to date (Nakayama, 1985). Wertheimer (1912) was one of the first to take up Exner's findings by systematically and thoroughly investigating the spatiotemporal parameters necessary to perceive apparent motion. The next few decades of research on motion perception mainly focused on further investigation of the spatiotemporal parameters and the factors affecting them. Starting with Korte (1915), and later Neuhaus (Neuhaus, 1930), who systematically investigated stimulus duration and spatial and temporal stimulus separation, the main aim was to find the optimal parameters for the perception of apparent motion. This led to the formulation of "Korte's laws", which describe some of the associations found between these parameters, and in particular, the relationship between interstimulus interval (ISI), spatial separation, and stimulus intensity. However, it soon became clear that there was no one set of parameters for apparent motion (Kolers, 1972) and that motion percepts depended on many other factors, although spatial and temporal separation were found to be more important then figural characteristics of the stimulus (Burt & Sperling, 1981). Other factors that affect the perception of apparent motion include stimulus-onset asynchrony (Kahneman & Wolman, 1970; Kolers, 1972), and stimulus variables such as contrast, size, duration, eccentricity, and colour (for a review see Grossberg & Rudd, 1992). One of the first who tried to answer the question of *how* the visual system perceptually matches corresponding stimuli across frames in apparent motion was Ullman (1979), who termed it the *correspondence* problem. When faced with an apparent motion stimulus, the visual system needs to identify the stimuli in successive frames "as representing the same object at different times, thereby maintaining the perceptual identity of objects in motion or change" (Ullman,

1979, p. 8). Ullman's *minimal mapping theory* is a model of how the visual system solves the correspondence problem by matching certain features (or *tokens*) across frames based partly on temporal and spatial parameters. This frame matching is believed to be a relatively low-level process (Dawson, 1991; Ullman, 1979) which was recently suggested to take place in the middle temporal area (MT/V5) in humans (Larsen et al., 2006).

Models of motion perception

Such investigations of apparent motion occurred in parallel with discoveries regarding visual receptive fields (Barlow & Levick, 1965; Hubel & Wiesel, 1959, 1962). Together they led to the formulation of various theories of motion perception, most of which included various kinds of directionally sensitive 'motion detectors' at a physiological level. Reichardt (1961) was the first to provide a model of such a motion detector, proposing a summative combination of spatial inputs over time. These physiological motion detectors are believed to be selectively tuned to spatial and temporal frequencies. While some have suggested the presence of a third type of detector tuned to different velocities (Reisbeck & Gegenfurtner, 1999), others suggest that the velocity tuning of the detectors is achieved by the detector being sensitive to a range of different spatial frequencies (Burr, 2002). Even though current models of motion detection are generally more elaborate than Reichardt's original proposal, his work provided the basis for most current models of motion perception (Sekuler et al., 1990; Sekuler, Watamaniuk, & Blake, 2002). Physiological motion detectors of this kind were considered by many to be insufficient to explain all phenomena of motion perception and particularly the perception of apparent motion. Separate mechanisms of motion perception were therefore proposed in various forms (Anstis, 1980;

Braddick, 1974, 1980; Julesz, 1971). One of the most influential explanations was by Braddick (1974, 1980) who proposed the short-range/long-range distinction with separate underlying processing mechanisms: a short-range process based on directionally sensitive neurons, and a more interpretive, higher-level long-range process. He suggested that short-range processes were involved in motion with small spatial displacements, short interstimulus intervals, and were governed by physiological motion detectors. Long-range processes on the other hand are involved with apparent motion over greater displacements or with more complex stimuli, and they are guided by higher order processes at a more cognitive level (what Anstis, 1980, called 'cognitive apparent motion'). Strong evidence supporting this view came from investigations using Ternus apparent motion (Ternus, 1926) and similar bistable displays (see Petersik, 1989, for a review).

David Marr (1982) further enhanced the field by proposing a computational approach to the study of motion perception in addition to the research at the physiological and behavioural levels. His work not only advanced the integration of 'top-down' versus 'bottom-up' approaches, but also allowed the field to become interdisciplinary by proposing different levels of study with computational, psychophysical and psychological approaches contributing (Smith & Snowden, 1994). Marr also provided the basis for many available motion detection models (Adelson & Bergen, 1985; van Santen & Sperling, 1985). A specific class of computational models are energy models, also called Fourier energy models because of the use of Fourier analysis in their computations (Adelson & Bergen, 1985; Heeger, 1987; A. B. Watson & Ahumada, 1985). While the different energy models vary at the mathematical level (in terms of the algorithms used), they are quite similar in their theoretical structure,

proposing separable spatiotemporal filters that detect orientation of stimuli in space-time. The motion energy of these stimuli is then computed using specific algorithms of the output of these space-time filters, using either linear on nonlinear combinations (Mather, 1994). Energy models have been successful in modelling how the visual system perceives continuous motion as well as many kinds of apparent motion phenomena. Indeed, such models provide a clear explanation of why the visual system can perceive apparent motion as continuous motion, because 'a continuous and a sampled stimuli share a great deal of spatiotemporal energy' (Adelson & Bergen, 1985, p. 286).

The limitations of energy models in fully accounting for motion perception became evident with the discovery of second-order motion stimuli (Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1989). These stimuli were clearly perceived by human observers, but existing Fourier models were not able to detect them. Cavanagh and Mather (1989) presented them as evidence for the invalidity of the short-range/long range distinction. Chubb and Sperling (1988, 1989) proposed that second-order motion was processed using a separate low-level motion perception mechanism, often called a *non-Fourier* channel, which is conceptually similar to the Fourier channel, but uses different computational strategies to detect motion. Some models, such as the spatiotemporal gradient model, (Johnston & Clifford, 1995; Johnston, McOwan, & Buxton, 1992) attempted to explain second-order motion using a single-channel theory. The spatiotemporal gradient model was successfully applied to first-order motion and a number of second-order stimuli. And indeed, some studies have failed to find psychophysical (Smith, Hess, & Baker, 1994), neurophysiological (Dupont, Sàry, Peuskens, & Orban, 2003; Seiffert, Somers, Dale, & Tootell, 2003),

and neurolopsychological (Greenlee & Smith, 1997) evidence for separate first- and second-order processes. However, the majority of available evidence strongly indicates that first-and second-order motion are processed by distinct mechanisms (Allard & Faubert, 2007; Ledgeway & Hutchinson, 2005; Ledgeway & Smith, 1994; Lu & Sperling, 1995a, 1995b; Mather & West, 1993; Smith, 1994a). This includes evidence that the two types of motion do not cancel each other (Scott-Samuel & Smith, 2000), show no cross adaptation (Nishida, Ledgeway, & Edwards, 1997), exhibit different visual evoked potential (VEP) latencies and psychophysical reaction times (Ellemberg, Lavoie et al., 2003), have distinct patterns of pursuit eye movement initiation (Lindner & Ilg, 2000), different spatial and temporal sensitivity functions (Hutchinson & Ledgeway, 2006), and developmentally mature at different rates (Ellemberg, Lewis et al., 2003). Available evidence from various neuroimaging studies (e.g., Noguchi, Kaneoke, Kakigi, Tanabe, & Sadato, 2005; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Sofue, Kaneoke, & Kakigi, 2003) and clinical human lesions studies (e.g., Vaina, Cowey, & Kennedy, 1999) further suggests that the two types of motion have different neural correlates. Based on this evidence, the main view at present is that first-and second-order motion are detected by separate mechanisms, at least initially. Recent evidence has indicated though that the inputs of the two mechanisms may later be integrated (Lindner & Ilg, 2000; Smith & Scott-Samuel, 2001; van der Smagt, Verstraten, Vaessen, van Londen, & Van de Grind, 1999; Zanker & Burns, 2001), and the nature and the site of this interaction is presently under investigation. While some evidence links the medial temporal area (MT/V5) with the integrating process of first- and second-order motion signals (Smith et al., 1998), others believe it occurs at an earlier processing stage, such as in V1 or V2 (Sofue et al., 2003).

In addition to the two low-level mechanisms believed to be involved in perception of first-and second-order motion, there is also evidence for higher-order strategies and processes contributing to, and perhaps modulating, motion perception. For example, mechanisms have been proposed that are based on high-level perceptual organisation of features, the origins of which are found in Ullman's *minimal mapping theory* (e.g., Dawson, 1991; Oyama, Naito, & Naito, 1994; Oyama, Simizu, & Tozawa, 1999). In addition, a strong attentional mechanism that is responsive to both first- and second-order stimuli (Smith, 1994a) has been proposed in motion perception (Cavanagh, 1992; Dick, Ullman, & Sagi, 1987; Horowitz & Treisman, 1994). Lu and Sperling (1995a, 1995b) provided a formal definition of a third, higher-order mechanism, in addition to the two separate low-level motion channels. This channel is described as a feature-tracking system modulated by selective attention. This higher-level or 'top-down' mechanism has been described as an active process, as opposed to the more passive mechanism of the low-level, 'bottom-up' channels (Cavanagh, 1991; Horowitz & Treisman, 1994; Scott-Samuel & Georgeson, 1999; Scott-Samuel & Hess, 2001; Smith, 1994a; Whitney, 2006). With the advent of these three motion channels, the validity of the two-tier short-range/long-range distinction in their original sense has been questioned (Cavanagh & Mather, 1989), although the definition has evolved to a broader meaning since it was first proposed by Braddick (Petersik, 1989, 1991). Nevertheless, Cavanagh (1991) argues that the distinction is redundant in light of the more recent first-and second-order distinction. Hence, while some recent papers still actively use the distinction (Grossberg & Rudd, 1992; Larsen et al., 2006; Zhuo et al., 2003), many avoid the distinction altogether, or use it in a descriptive, rather than an absolute sense (Horowitz & Treisman, 1994).

The neurology of motion perception

Motion pathways

In parallel with the development of models of motion perception, neurophysiological and anatomical studies in primates and the more recent neuroimaging studies in humans have greatly increased our understanding of neural correlates of visual perception and motion perception pathways. The distinction between two independent, parallel pathways (see Figure 6) for the perception of motion (*parietal* or *dorsal* pathway) and the perception of colour and form (*temporal* or *ventral* pathway) is now well-established (see Maunsell & Newsome, 1987, for a review), although recent evidence suggests that there is some involvement of the ventral pathway in motion perception regarding colour (Edwards & Badcock, 1996; Gegenfurtner & Hawken, 1995; Metha, Vingrys, & Badcock, 1994; Takeuchi, De Valois, & Hardy, 2003) and form (Tse & Logothetis, 2002; Zhuo et al., 2003).

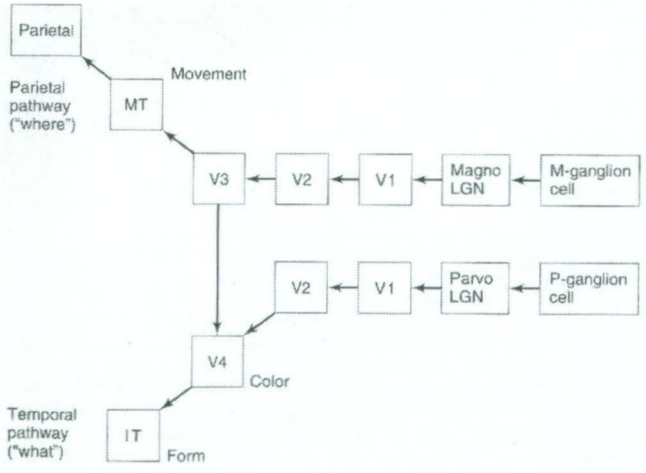

Figure 6. Simplified diagram of the visual pathways (from right to left). The parietal pathway flows from M-ganglion cells through the LGN, striate cortex V1 and on to extrastriate areas V2, V3 and via the medial temporal area (MT) to the parietal cortex. The temporal pathway includes extrastriate areas V4 and the inferotemporal cortex (IT) and on to the temporal lobes (from Goldstein, 2002)

The motion perception pathway follows a hierarchical structure, from the retinal parasol cells via the magnocellular cells of the lateral geniculate nucleus (LGN) to the striate and extrastriate cortex, becoming increasingly larger and more complex at each stage of processing (S. Anderson, 1997; Maunsell & Newsome, 1987). From the LGN, the magnocellular cells project to layers 4cα and 4B of V1, although there is evidence of some parvocellular input to the motion perception pathway at this level (K. K. De Valois, Cottaris, Mahon, Elfar, & Wilson, 2000; Maunsell, Nealy, & De Priest, 1990). Directionally selective cells in V1 then project to the middle temporal area (MT) both directly and indirectly via areas V2 (Maunsell & Newsome, 1987), and V3 (Newsome & Paré, 1988). MT neurons in turn project to other areas, including the medial superior temporal (MST) area and the lateral and ventral intraparietal (LIP and VIP) areas (Maunsell & Van Essen, 1983a) and beyond.

The neuro-anatomy of motion perception

In primates, various anatomical, psychophysiological and lesion studies have singled out MT as an area of particular importance for motion perception (see Snowden, 1994, for a review). More than 80% of neurons in MT are direction selective (Maunsell & Van Essen, 1983a; Mikami, Newsome, & Wurtz, 1986a), the activity of neurons in MT (as well as V1) closely matches monkeys' psychophysical performance in motion detection (Britten, Shadlen, Newsome, & Movshon, 1992; Newsome, Mikami, & Wurtz, 1986), including their spatiotemporal limits for apparent motion (Mikami, Newsome, & Wurtz, 1986b). Lesions to MT temporarily elevate motion perception thresholds (Newsome & Paré, 1988). The human equivalent to primate area MT (area MT or V5) was identified using positron emission tomography (PET) and magnetic resonance imaging (MRI) (J. D. G. Watson

et al., 1993) and functional MRI (fMRI) (Tootell, Reppas et al., 1995), although there is some variability in its precise location on the human cortex (J. D. G. Watson et al., 1993). Numerous studies have since established the crucial role of MT/V5 in human motion perception (see Vaina, Cowey, Eskew, LeMay, & Kemper, 2001, for a review), and have shown that its activation is not purely stimulus driven, but can reflect motion aftereffects (Tootell, Rappas et al., 1995) and actual conscious perception of motion (Muckli et al., 2002) as well as apparent and imagined motion (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998). The traditional view is that MT/V5 neurons integrate motion over wider areas of the visual field (Andersen, 1997), as it has significantly larger visual receptive fields than area V1. The integrated motion signals that MT passes on to other areas then provide the basis on which decisions about appropriate responses (e.g., eye movements) are made (Andersen, 1997). Furthermore, MT has been implicated in the encoding of velocity (Kawakami et al., 2002; Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983b; Snowden, 1994). Recent evidence suggests that neurons in V1 and MT/V5 are similarly direction selective but vary in the range of velocities they are responsive to (A. K. Churchland, Priebe, & Lisberger, 2005). Although there is some overlap in velocities, there is evidence that MT/V5 neurons are more responsive to higher velocities compared with V1 neurons (A. K. Churchland et al., 2005; Gegenfurtner & Hawken, 1995; Newsome et al., 1986).

The medial superior temporal area (MST) is also an important area for motion processing. Although different areas of MST have distinct preferences with regard to what motion stimuli they respond to, overall MST is believed to be responsible for the processing of more complex motion (A. K. Churchland et al., 2007) including

expansions, contractions, and spiral motion (Andersen, 1997; Maunsell & Newsome, 1987; Snowden, 1994), as well occluded motion (Assad & Maunsell, 1995), and there is some evidence that MST neurons prefer faster velocities (A. K. Churchland et al., 2007). MST, together with MT, has also been shown to play a crucial role in the processing of optic flow (Vaina, 1998). In addition to MT and MST, a number of other areas have been identified to be involved in motion perception. Areas V2 and V3 both have some directionally sensitive cells and project to MT (Maunsell & Newsome, 1987; Newsome & Paré, 1988), and there is some evidence that V3 is more strongly involved in processing second-order motion stimuli (Smith et al., 1998). Area V3a has also been linked to perception of coherent motion (Aspell, Tanskanen, & Hurlbert, 2005), together with other parts of the superior temporal sulcus (STS), which has also been linked to the perception of biological motion (Grossman et al., 2000; Lange & Lappe, 2006; Servos, Osu, Santi, & Kawato, 2002). Intraparietal areas LIP and VIP, which receive information from MT and MST (Maunsell & Van Essen, 1983a), are believed to be the sites for perceptual decision making based on visual signals that are integrated for decisions concerning appropriate visually guided movements (Hanks, Dittrich, & Shadlen, 2006; Shadlen & Newsome, 1996, 2001).

Recent advances in brain imaging techniques have also provided further evidence regarding the distinct mechanisms underlying the perception of first- and second-order motion. Areas V1, V2, MT/V5, and MST have reliably been found to be activated in response to both first- and second-order motion stimuli (Albright, 1992; Dupont et al., 2003; Noguchi et al., 2005; Seiffert et al., 2003; Smith et al., 1998; Sofue et al., 2003), and these areas have therefore been established to be involved in

processing both types of motion. However, Ashida, Lingnau, Wall, and Smith's (2007) findings suggested that different areas of MT/V5 and V3A may process the different types of motion, as there was not fMRI cross-adaptation. There is also some evidence that areas V3 and VP are activated more strongly in second-order motion perception (Smith et al., 1998) and that STS, is only involved in second-order motion perception (Noguchi et al., 2005; Vaina et al., 1999). However, such findings are inconsistent and tend to vary somewhat with the kind of motion perception task used (Noguchi et al., 2005).

Motion perception and eye movements

Motion perception and smooth pursuit eye movements

Visual perception and visually guided motor action are sometimes viewed as discrete processes with separate underlying mechanisms and neurology (Ganel & Goodale, 2003; Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991; Loomis, Da Silva, Fujita, & Fukusima, 1992; Milner & Goodale, 1993), with visual perception seen to precede visually guided motor action. Similarly, it is sometimes suggested that motion perception and smooth pursuit eye movements also have separate underlying mechanisms (Bridgeman, Kirch, & Sperling, 1981; Mack et al., 1979; Mack et al., 1982), although many recognise that the two are, at the very least, very tightly linked (Ilg, 2008; Keller & Heinen, 1991). Even if not explicitly stated, most models of pursuit also imply a separation of motion perception and pursuit by conceptualising pure retinal events as driving pursuit (e.g., Krauzlis & Lisberger, 1994; Lisberger et al., 1987; D. A. Robinson et al., 1986). In recent years, however, the commonalities of motion perception and eye movements are being investigated

more frequently, partly to increase our understanding of the dynamic relationship between perception and action in general (Masson & Mestre, 1998).

Initial indications that motion perception and smooth pursuit may share underlying processes came from evidence that perceived motion, rather than just retinal motion on the retina (retinal slip) may be driving pursuit (e.g., Steinbach, 1976; Wyatt & Pola, 1979; Yasui & Young, 1975; see Chapter 2). Numerous psychophysical and behavioural experiments have since been conducted comparing motion perception and pursuit. Perceptual discrimination of speed and direction is limited by noise in neural activity in sensory areas and such estimates therefore fluctuate from trial to trial (Newsome, Britten, & Movshon, 1989). These trial-by-trial fluctuations have been found to be highly similar and correlated between perceptual discrimination and pursuit performance (Beutter & Stone, 2000; Krauzlis & Adler, 2001; Stone et al., 2000; Stone & Krauzlis, 2003). The overall motor variation for pursuit and perception in discriminating direction, speed, and timing has also been found to be highly similar in perceptual and pursuit tasks (Osborne, Lisberger, & Bialek, 2005). Furthermore, perceptual decisions and smooth pursuit eye movements have been shown to behave in near identical ways in response to directional biases (Beutter & Stone, 1998), to manipulation of complex motion conditions (Stone et al., 2000), and to various motion aftereffects (Braun et al., 2006). Perceptual and pursuit reversals have also been shown to be nearly identical for a bi-stable apparent motion paradigm (Madelain & Krauzlis, 2003), and the same illusionary speed discrimination effect has been revealed to be the cause for motion perception and smooth pursuit of apparent motion (A. K. Churchland & Lisberger, 2001). Motion perception and pursuit also have similar thresholds for direction discrimination (Watamaniuk & Heinen, 1999) and

velocity discrimination (Kowler & McKee, 1987). These relationships are consistent with findings using other visually guided motor behaviours that show that perception and action process velocity and position information in very similar ways (Bosbach, Prinz, & Kerzel, 2004; Smeets & Brenner, 1995). Smooth pursuit eye movement performance has also been found to decrease with decreasing contrast levels in the same way as perceptual performance (Spering et al., 2005). Human perception and smooth pursuit of moving targets are both more sensitive to changes in speed than in acceleration (Watamaniuk & Heinen, 2003) and both are equally affected by cognitive expectation (Krauzlis & Adler, 2001). Furthermore, perceptual performance has significantly better direction discrimination for cardinal (i.e., horizontal and vertical) than for oblique (diagonal) directions, a phenomenon called anisotropy, which has been found in maintained smooth pursuit (Krukowski & Stone, 2005). Earlier studies of open-loop pursuit had failed to find pursuit anisotropies (A. K. Churchland, Gardner, Chou, Priebe, & Lisberger, 2003). On the other hand, some studies have reported differences between motion perception and pursuit. For example, Bridgeman, Gemmer, Forsman, and Huemer (2000) found a dissociation between perception and visually guided action, with perception being controlled by a cognitive representation, while action was driven by a sensorimotor representation. However, their study employed a manual motor task and similar results using smooth pursuit eye movements (Schweigart, Mergner, & Barnes, 2003) were interpreted by the authors as evidence for a close interrelationship between perception and smooth pursuit. Nevertheless, there is some indication that the close agreement between perception and pursuit may not hold for very complex motion tasks, such as those involving segmentation of target object motion from context motion (Spering & Gegenfurtner, 2007b). Taken as a whole, these findings provide strong evidence for a

link between motion perception and smooth pursuit eye movements and indicate that they share common neural motion processing mechanisms and signals (e.g., Ilg & Thier, 2008; Stone et al., 2000). The extent of the signal sharing is not yet entirely clear, and the available evidence does not completely rule out that perception and pursuit are controlled by separate parallel pathways (e.g., Goodale & Milner, 1992), which are merely highly similar in location and nature.

With regard to underlying neural correlates of the shared sensory processing of motion perception and smooth pursuit eye movements, Dobkins, Stoner, and Albright (1998) were the first to demonstrate that the parallel changes in perception and pursuit were associated with neurophysiological responses in MT neurons in monkeys. Separate investigations into the neurological correlates of motion perception (see Chapter 5) and smooth pursuit eye movements (see Chapter 3) revealed that very similar structures are involved in both processes (Keller & Heinen, 1991; Krauzlis & Stone, 1999; Leigh & Zee, 1999) and that the motion processing pathways provide multiple inputs to the pursuit system (Lisberger et al., 1987). In particular, areas MT/V5 and MST have been strongly implicated in playing a crucial role in both motion perception (Britten et al., 1992; Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983a; Newsome et al., 1986) and smooth pursuit (Bremmer, Ilg et al., 1997; Dürsteler & Wurtz, 1988; Komatsu & Wurtz, 1988; Lisberger & Movshon, 1999; Priebe et al., 2001). Parietal areas (LIP and VIP) have been associated with both motion perception (Maunsell & Van Essen, 1983a; Shadlen & Newsome, 1996, 2001) and smooth pursuit (Ohkubo et al., 2000; Petit & Haxby, 1999), and have been suggested as the sites at which decisions are made on actions, based on the perceptual signals (Hanks et al., 2006; Shadlen & Newsome, 1996,

2001). However, motion perception and pursuit are rarely measured simultaneously during neural imaging studies. One exception is Barton and colleagues (Barton, Simpson et al., 1996), who used fMRI to measure cortical activity in response to motion perception and pursuit. They found that the same cortical areas (extrastiate and lateral occipitotemporal cortex) were activated during both tasks, with a generally greater activation in response to smooth pursuit compared with motion perception. However, the two tasks used differed significantly with regard to their target stimulus, motion direction and velocity, which makes it difficult to interpret the findings. Another study by Barton, Sharpe, and Raymond (1996) compared patients with various clinical lesions, finding a double dissociation of ability: some patients had impaired motion perception but normal smooth pursuit, while others had normal motion perception and impaired smooth pursuit. As the authors pointed out though, their motion perception and pursuit tasks were not comparable, involving vastly different types of motion processing (global versus local motion). Furthermore, it has been shown that pursuit deficits produced by MT/MST lesions in monkeys are initially profound, but that pursuit based on position information is still possible (Dürsteler & Wurtz, 1988; Dürsteler et al., 1987) and that general pursuit ability recovers within days (Yamasaki & Wurtz, 1991), in part because there are multiple compensating pursuit pathways (see Chapter 3). To date, there are no studies that directly compare the neural correlates of motion perception and pursuit by simultaneously measuring both responses on the same tasks. Doing so would further our understating of whether motion perception and smooth pursuit eye movements are based on the same or merely similar but separate pathways with adjoining neural areas. Given the poor spatial resolutions of fMRI and the fact that even neurons in close proximity can be part of separate pathways (Yoshimura & Callaway, 2005),

even such studies will not be able to give us a definite answer. Even though no one single study will be able to provide a definite answer to the question of whether motion perception and pursuit have shared or separate neural pathways, the current accumulated evidence is in favour of the more parsimonious explanation, of shared pathways. Current evidence strongly suggests that at least up to areas MT/MST, sensory pathways and signals are shared between the motion perception and smooth pursuit, and with additional shared areas likely in the parietal cortex, where perceptual decisions for guided behaviour are believed to be made (Shadlen & Newsome, 1996, 2001).

Motion perception and pursuit eye movements therefore appear to share underlying motion processing mechanisms and the perception of motion affects pursuit eye movements. However, there is also evidence to suggest that eye movements in turn affect motion perception. Retinal signals relating to target motion and extraretinal signals relating to pursuit eye movements are believed to be added during pursuit to a combined motion perception signal (Pola & Wyatt, 1989; Souman, Hooge, & Wertheim, 2005a), although in a more complex than just linear fashion (Souman, Hooge, & Wertheim, 2005b). Velocity judgements have been shown to be affected by pursuit eye movements (Brenner & van den Berg, 1994; Turano & Heidenreich, 1999). Also, perceived direction of motion over the whole 360 degree range is affected by pursuit eye movements (Souman et al., 2005a), although not when comparing cardinal versus oblique directions (Krukowski, Prirog, Beutter, Brooks, & Stone, 2003). Smooth pursuit can also enhance the perception of coherent motion (Greenlee, Schira, & Kimmig, 2002), and constrain visual perception of particularly ambiguous situations to assist their interpretation (Hafed & Krauzlis, 2006).

Motion perception and saccades

While there is ample evidence that motion perception and smooth pursuit eye movements are very tightly linked and even share many underlying mechanisms, there is only a weak link between motion perception saccadic eye movements because saccades are generally triggered in response to position signals. However, as discussed in Chapter 4, saccades to moving targets, such as in saccadic tracking, use visual motion information, particularly as it relates to retinal velocity (Blohm et al., 2003; De Brouwer, Missal et al., 2002; De Brouwer et al., 2001; De Brouwer, Yuksel et al., 2002; Guan et al., 2005; Schreiber et al., 2006), and lesions to MT cause deficits in saccades to moving targets (Newsome et al., 1985). Given that saccades and smooth pursuit may share many neural mechanisms (see Chapter 3) and smooth pursuit and motion perception may have shared visual processes, it is very likely that the visual motion processing underlying saccades to moving targets also share these neural signals. Hence, visual motion processing, and in particular the extrapolation of retinal velocity, affects saccadic eye movements to moving targets. However, saccadic eye movements in turn also affect visual motion perception. As discussed in Chapter 2, motion perception may be suppressed during saccadic eye movements (Burr et al., 1999; Diamond et al., 2000; Ilg & Hoffmann, 1993; J. Ross et al., 2001; Sperling, 1990), and there is an enhancement of motion perception at the end of a saccade (Gardner & Lisberger, 2001; Lisberger, 1998; Schoppik & Lisberger, 2006) or immediately after (Ibbotson et al., 2007; Reppas et al., 2002). However, other studies have found that motion perception can be negatively affected by saccades (C. Lee & J. Lee, 2005), showing a motion processing bias in the direction opposite to the

saccade, both before (J. Lee & C. Lee, 2005) and up to 100ms after a saccade (Park et al., 2001).

In summary, motion perception affects smooth pursuit and may even affect saccadic eye movements and both in turn influence motion perception. This suggests the existence of shared processes for visual motion perception and smooth pursuit and saccadic eye movements, or at least a very tight coupling. It is therefore important that oculomotor models incorporate the higher-order and non-linear visual processing associated with perception and similarly, models of visual perception need to incorporate the role of eye movements (Stone, Miles & Banks, 2003). This thesis aims to further investigate the suggested link between motion perception and visual tracking.

Summary, rationale and aims of the thesis

Saccadic and smooth pursuit eye movements work together when visually tracking a target. Saccades are fast, abrupt eye movements which aim to bring an object onto the fovea, while smooth pursuit eye movements are slow and smooth movements that aim to retain a moving object on the fovea. A lot is known about how saccadic and smooth pursuit eye movements are generated (see Chapter 2) even though there are some differences between the specific models available for the generation of saccades and smooth pursuit. Saccadic eye movements are more ballistic, although there is some online feedback to the system with regard to the spatial position and the velocity of the objects during the long latency period. Nevertheless, once a saccade is triggered, this information can not change the initiated saccade trajectory, but can be

used to plan the subsequent saccade. Smooth pursuit eye movements on the other hand have continuous information feedback, comparing the movement of the target with the movement of the eyes, at least after the initial 100ms pursuit initiation phase. The neurological correlates of oculomotor control are also fairly well established (Chapter 3), although more recently the question has arisen whether saccadic and smooth pursuit eye movements share some underlying processes and mechanisms or may even be two different outcomes of a single mechanism (Krauzlis, 2004, 2005; Krauzlis & Stone, 1999; Orban de Xifry & Lefèvre, 2007; see Chapter 3).
During visual tracking, saccadic and smooth pursuit eye movements collaborate closely and the precise mechanisms for this are not yet known (see Chapter 4). The most common way that visual tracking is conceptualised is that at slow target velocities smooth pursuit alone is sufficient to track a target. At faster target speeds the eye increasingly lags behind the target and the resulting position error triggers a catch-up saccade (see Chapter 2). However, only very narrow velocity ranges have generally been measured, the lower speed limit of smooth pursuit has never been investigated, and the saccadic tracking component is frequently ignored. The nature of the relationship between motion perception and visual tracking is also not yet established, although the available evidence indicates that motion processing mechanisms are shared for perception and eye movements (Chapter 5).

Using apparent motion stimuli to study visual tracking have been very promising (Chapter 4), as they allow breaking down the target stimulus into its spatial and temporal parameters, and therefore enable us to separate the saccadic and smooth pursuit tracking components. In normal observers there has not yet been a systematic

study investigating and comparing different apparent motion paradigms at a range of target speeds.

Accordingly, this thesis aims to investigate the understanding of saccadic and smooth pursuit components of visual tracking and their relationship to motion perception in the following ways: First, by systematically examining visual tracking over a range of velocities, using both continuous and apparent motion paradigms, in order to distinguish the separate contributions of saccadic and smooth pursuit tracking components, and examine the nature of their interplay during visual tracking. Second, by comparing two apparent motion paradigms (jumping-dot and slashed motion) with continuous motion stimuli in the generation of visual tracking eye movements. Finally, by a direct comparison of both continuous and apparent motion elicited visual tracking with visual motion perception, using stimulus parameters that facilitate both visual tracking and visual motion perception under similar conditions.

Chapter 6

The saccadic and smooth pursuit components of visual tracking of continuous visual motion stimuli (Experiment 1)

An important focus of this thesis is the investigation of visual tracking of apparent motion. In order to accurately interpret findings obtained with apparent motion stimuli it is crucial that visual tracking in response to continuous motion is accurately measured, described, and understood. Although visual tracking of continuous motion has been extensively studied and quantified over the years using a variety of different motion stimuli and tasks (as outlined in Chapter 4) the saccadic and smooth pursuit components of visual tracking were traditionally combined in these investigations, which led to a general overestimation of smooth pursuit ability (R. H. S. Carpenter, 1988). Only after Bahill, Iandolo and Troost (1980) advocated a separation of the two tracking components did visual tracking research start to uncover the real performance of the smooth pursuit system alone, but the saccadic component of visual tracking continued to be largely ignored, with researchers either removing the saccades (e.g., Handke & Büttner, 1999; Moschner & Baloh, 1994), or simply counting the number of saccades (e.g., Ettinger et al., 2003) without close examination of their characteristics. Hence, while there are certainly numerous studies outlining smooth pursuit parameters in normal observers, many either report an overestimation of smooth pursuit performance by reporting dual-mode tracking (e.g., Schalen, 1980; Sharpe & Sylvester, 1978), or only provide half the picture of visual tracking, because they ignore the saccadic contribution. Recently, interest in the interplay of saccades and pursuit during visual tracking has increased (see Chapter

4) because the possibility of shared inputs to the two eye movements is being investigated (see Chapter 3). This has resulted in progress in relation to the examination of the saccadic component of visual tracking, but the main focus is generally on the interaction between the two eye movements, rather than describing and quantifying saccadic eye movements during visual tracking. Although such studies have greatly increased the current knowledge of how ongoing smooth pursuit eye movements affect saccades and vice versa (see Chapter 4), most of these studies have examined a specific type of saccade within the tracking response (De Brouwer, Yuksel et al., 2002), had non-human subjects (De Brouwer et al., 2001), or focused on the influence of pursuit velocity on saccade characteristics (De Brouwer, Missal et al., 2002).

Early studies that used dual-mode tracking gain as a measure generally reported high pursuit gain, with values ranging from 0.9-1.0 for target velocities up to 40.0 deg/s (Schalen, 1980; Sharpe & Sylvester, 1978). Even after saccades were removed from dual-mode tracking, single-mode pursuit gain close to 1.0 has been reported to represent normal single-mode pursuit performance (e.g., Ettinger et al., 2003; Wirtschafter & Weingarden, 1988), although the tested target velocities varied greatly and there is no consensus for what actually constitutes normal pursuit gain. It is frequently reported that approximately 8% of normal observers have abnormal smooth pursuit, based on Holzman's findings (Holzman et al., 1974; Holzman, Soloman, Levin, & Waternaux, 1984), although depending on what definitions are used, values range from 0-16 % (Clementz & Sweeney, 1990). Some perceive single-mode pursuit gain below 0.85 as abnormal, while others state that a gain of 0.7 represents the low end of normal for fast stimulus velocities (above 20.0 deg/s; D. A.

Robinson et al., 1986). After reviewing the available literature, Pola (2002) reported that single-mode pursuit gain of 0.6-0.95 can be considered normal, depending on task conditions and target velocity. Furthermore, the literature reports that single-mode pursuit gain is highest for slow target velocities (below 20.0 deg/s) and then decreases as a function of velocity, with a parallel increase in saccade frequency to compensate for the increased lag of the eye behind the target. This notion is partly based on very early studies though (e.g., Schalen, 1980; Westheimer, 1954), which failed to separate the pursuit and saccadic tracking components, and there have been few studies that have systematically investigated single-mode pursuit gain over a wide range of velocities (see Chapter 2). Hence, it has not been established what constitutes optimal velocity for single-mode pursuit, and many studies only use one velocity with values generally ranging from 5.0-30.0 deg/s. Lower velocity limits for smooth pursuit eye movements have not been investigated, even though the findings of some of the few studies that have measured target speeds below 5.0 deg/s have suggested that smooth pursuit eye movements may deteriorate at very slow velocities (Carl & Gellman, 1987; M. M. Churchland & Lisberger, 2000; Murphy, 1978; Spering et al., 2005), and Lamontagne (1973) suggested that a lower velocity limit would exist for smooth pursuit of apparent motion.

With regard to saccadic eye movements during visual tracking, the findings are even less clear. The literature commonly reports that an increase in target velocity is associated with increased saccade frequency and saccade amplitude (Ciuffreda & Tannen, 1995; Eckmiller, 1987; Hallett, 1986; Lisberger et al., 1987; Pola, 2002; Westheimer, 1954), as well as larger saccade duration and peak velocity (Eggert et al., 2005). It was recently suggested that the characteristics of saccadic eye

movements during visual tracking should be corrected for target velocity to remove the pursuit dynamics (De Brouwer, Missal et al., 2002), and other studies have since applied these corrections (e.g., Eggert et al., 2005). Also, many studies of normal visual tracking only report either saccade frequency or saccade characteristics, even though the two should not be interpreted in isolation (R. G. Ross, Olincy, & Radant, 1999). In studies investigating abnormal visual tracking, saccade frequency is generally the main measure used to describe the saccadic component of visual tracking. For example, apart from decreased single-mode pursuit gain, increased saccade frequency is the only consistent feature of disordered tracking in schizophrenia (O'Driscoll & Callahan, 2008), which highlights how crucial it is to ensure that saccades during visual tracking are accurately identified, measured and reported. Some attention has also been given to dividing saccades generated during visual tracking into categories (i.e. catch-up saccades, anticipatory saccades, leading saccades, etc.), but there are not yet clearly established classification criteria, and there is some evidence that the characteristics of the different types of saccades during tracking do not actually differ once they are corrected for pursuit velocity (De Brouwer, Missal et al., 2002, see Chapter 4). It is also important to carefully select the criteria used to identify saccades during visual tracking, and although these can vary greatly, more recent studies generally report how saccades are selected, which facilitates consistency across studies. Usually a combination of velocity, acceleration, and amplitude criteria are used to maximise saccade detection, while excluding artefacts (see e.g., O'Driscoll et al., 2000). To date, however, very little attention has been given to the way in which saccade frequency during visual tracking is reported, despite it currently being the main measure of saccade performance. Some studies report the number of saccades per second or minute (Ettinger et al., 2003; Katsanis et

al., 2000; Randal G. Ross et al., 1999; Schalen, 1980; Sharpe & Sylvester, 1978), while others report the absolute number of saccades (Avila, Weiler, Lahti, Tamminga, & Thaker, 2002; Chan, Codd, Kenny, & Eustace, 1990; Van Gelder et al., 1990) or the number of saccades per cycle (Slaghuis et al., 2007a). More recently, Ross and colleagues (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999) reported the percent of total eye movements consisting of saccades in terms of the distance covered by saccadic eye movements, which accounts for saccades of varying amplitudes. A similar measure reporting the time spent in saccades versus smooth pursuit was subsequently used in other studies (Avila, Sherr, Hong, Myers, & Thaker, 2003; Avila, Weiler et al., 2002). A large number of studies, however, simply report the number of saccades without further specifying their measure (e.g., Avila, Hong, Moates, Turano, & Thaker, 2006; S. B. Hutton et al., 2001; Lisberger et al., 1987), although their numbers suggest that they generally report the absolute numbers of saccades. This frequent failure to specify what frequency criteria is used matters less for those studies using only one target velocity (e.g., Levy et al., 2000; Radant & Hommer, 1992; D. E. Ross et al., 1997; R. G. Ross et al., 2002; Schulze et al., 2006; Sweeney, Brew, Keilp, Sidtis, & Price, 1991), but when comparing saccade frequency across more than one target velocity, the temporal and spatial criteria change greatly. It is therefore essential to define whether the reported saccade frequency relates to the number of saccades generated within a specific timeframe or a specific spatial distance. Even measures reporting the ratio of saccadic versus pursuit eye movements can be time-based or distance-based, comparing either the time spent in saccadic versus smooth pursuit eye movements (Avila et al., 2003; Avila, Weiler et al., 2002) or comparing the distance covered with

saccadic versus smooth pursuit eye movements (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999). To date, the question of how to best quantify saccades during visual tracking has not been formally investigated and the different measures have never been directly compared over a range of target velocities.

Existing studies have provided a good overview of what variables affect visual tracking, including many task and stimulus characteristics, such as target velocity, stimulus size, luminance, and trajectory amplitude (see Chapter 2 for a detailed review). Sex and age are potential observer characteristics that may also affect visual tracking, but there have been surprisingly few studies that have directly investigated sex differences. Even though studies are frequently matched for gender, there is only sparse evidence that males have better visual tracking than females (T. J. Hutton, Nagel, & Loewenson, 1983; Kuechenmeister, Linton, Mueller, & White, 1977), consistent with their superior performance in other motor tasks (Nalçaci, Kalaycioglu, Çiçek, & Genc, 2001; Telford & Spangler, 1935), while other studies have actually found better visual tracking for female observers (Kelley & Bakan, 1999). Age effects have more consistently been found, with most studies reporting an age-related decline in smooth pursuit performance, consisting of a decrease in single-mode pursuit gain and acceleration, and an increase in distractibility, variability, and velocity latency (Handke & Büttner, 1999; S. R. Kaufman & Abel, 1986; Moschner & Baloh, 1994; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; Sharpe & Sylvester, 1978; Spooner, Sakala, & Baloh, 1980). The performance on saccadic tasks also declines with age, with saccades generated by older people having slower peak velocity, longer latency and decreased accuracy (Irving, Steinbach, Lillakas, Babu, &

Hutchings, 2006; Moschner & Baloh, 1994). Age effects for saccadic eye movements during visual tracking have rarely been examined, although there is some evidence of an increase in the frequency of catch-up saccades (Chan et al., 1990; T. J. Hutton et al., 1983; Morrow & Sharpe, 1993) and square-wave jerks (S. R. Kaufman & Abel, 1986) in elderly observers. Overall, studies reliably show age effects from about the age of 60-70 years, consistent with similar findings in manual tracking tasks (Kerr, Blais, & Toward, 1996), but there are large differences in what constitutes a 'young observer' and ages vary from 18-45 years. Although there is some evidence that performance on saccadic tasks is unaffected by age within this range (Irving et al., 2006), there is little research comparing visual tracking of observers within this range.

In summary, while visual tracking of continuous motion has been previously investigated, this has rarely been done using a wide range of target velocities and the saccadic component of visual tracking has generally been neglected or ignored. Also, saccade frequency has been reported in inconsistent ways, and to date, there has been no study systematically comparing different measures for quantifying saccades during visual tracking. In addition, the interplay between saccadic and smooth pursuit eye movements during visual tracking has not yet been thoroughly described and examined in visual tracking of continuous motion at a range of target velocities. Also, in order to investigate and accurately interpret visual tracking of apparent motion stimuli, which is an important focus of this thesis, it is important to fully describe and understand visual tracking of continuous motion under similar experimental conditions.

The aim of the current study was therefore to quantify smooth pursuit and saccadic components of visual tracking of continuous motion stimuli at a range of stimulus velocities, in part to provide a sound baseline study for subsequent investigations of visual tracking of apparent motion, with particular interest on the saccadic component, including an evaluation of different measures used to quantify saccades during visual tracking.

Based on the literature the following hypotheses are proposed:

1. It is expected that dual-mode tracking gain will remain largely unaffected by target velocity (e.g., Schalen, 1980; Sharpe & Sylvester, 1978).
2. Single-mode pursuit gain is expected to be highest for slow velocities and decrease with increasing target velocity, with a parallel increase in saccade frequency to compensate for the increase in lag of the eyes behind the target (e.g., R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995).
3. This increase in saccade frequency with increasing target velocity should be evident for all saccade frequency measures.
4. An increase in saccade amplitude, duration and peak velocity is expected with increasing target velocity (e.g., Eggert et al., 2005; Hallett, 1986; Westheimer, 1954).
5. A decrease in smooth pursuit performance with increasing age is expected (e.g., Moschner & Baloh, 1994).
6. Due to the variable findings regarding sex effects on visual tracking reported in the literature no hypotheses were made regarding this variable.

Method

Participants

Fifteen males and fourteen females were classified into three age groups (18-24; 25-29; 30-39 years) with five males and five females in each group (apart from only four females in the 30-39 year age-group). All participants self-reported that they were free of psychiatric and neurological disorders, and that they did not smoke cigarettes or use illicit drugs, using a brief screening questionnaire, which is presented in Appendix A. Participants who did not meet these criteria were excluded from the study, as were those with vision less than 6/6 (corrections with contact lenses were accepted), which was tested using a *Snellen acuity chart.* The eye movement recording equipment did not allow participants to wear glasses. An information sheet was provided and written informed consent was obtained, and the study had approval from the *Tasmanian Social Science Human Research Ethics Committee.*

Eye movement stimuli

A single black dot of 0.25 deg of visual angle on a white background was presented on a Sony Trinitron CPD-G520 colour computer display monitor, with a frame rate of 100 Hz. The dimensions of the screen were 21.8 deg horizontally x 16.7deg vertically when viewed at a distance of one metre, resulting in a motion trajectory of 20.0 deg at 1.0 m viewing distance. The target stimuli were generated using the Cambridge Research Systems Visual Stimulus Generator (VSG 2/5) and the Cambridge Research Systems Eye Trace Program Version 3.0 (copyright 1996-2004), which also recorded eye movements. Eye movements were recorded in a dark room with the screen dimly

illuminated from the front by a fluorescent light source which sat hidden within a screen surround cover, resulting in an overall luminance of 24.8cd/m².

Visual tracking of continuous motion was recorded at nine constant stimulus velocities (2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0°/s), and a step-ramp procedure was used for the initiation of the target movement, with the target jumping horizontally from a central position to10.0 deg to the left, where it then started moving to the right at constant target speed. At either end of the monitor (±10.0 deg) it paused for 200ms before changing direction. Due to constraints of the visual tracking software, target velocities were presented in increasing order.

Procedure

Four full-cycles of visual tracking (160.0 deg) were recorded for each target velocity, and data was collected in one session of approximately 30minutes, including regular rest periods. A chin rest with a horizontal bite board was used to minimise participants' head movements and participants were instructed to keep their eyes on the target at all times during recording.

Eye movement recording

Eye movements were recorded by an infra-red limbus reflection device (Skalar, IRIS, Skalar Medical B.V.) with a linear range of 20.0 deg and an optimal resolution of 2.0 min arc, which records data with a temporal resolution of 200 Hz. For convenience, eye movements were only recorded from the right eye. The calibration for the eye movement recording was obtained by recording a total of eight saccades to the left and to the right of the central fixation point, with saccades 2.0, 4.0, 6.0, and 8.0 deg amplitude, and a new calibration was completed after each rest break.

Eye movement analysis

The software package MatLab 6.0.0.88 Release 12 (The Math Works Inc., 2000) was used to process and analyse eye movements. The first half cycle of each target velocity was excluded in order to allow participants to adjust to each new velocity, leaving 3.5 cycles for analysis for each stimulus velocity. The program automatically selected from 250ms into the visual tracking trace (to exclude open-loop pursuit) until 50ms before the next pause, and all eye blinks and square-wave jerks were removed manually by applying consistent criteria. For single-mode pursuit measures all saccades were removed automatically, as well as a period of 10ms before and 10ms after each saccade and pursuit segments shorter than 50ms (Gegenfurtner, Xing, Scott, & Hawken, 2003). Saccades were detected using an acceleration criterion (750 deg/s^2), a criterion taking into account velocity of ongoing pursuit in a 100ms window prior to the saccade, as well as an amplitude criterion of 0.25 deg. Most previous studies have used acceleration criteria of 500, 750 or $1000deg/s^2$, and the medium value was chosen, although a visual comparison of the three criteria did not show any differences between them. The velocity criterion identified saccades whose velocity exceeded the average velocity of the preceding 100ms by more than 30.0 deg/s (e.g., Ettinger et al., 2003; O'Driscoll et al., 2000), and even though windows of 100ms and 50ms have been used in previous research, 100ms was selected, because it is closer to the planning time of a saccade. An amplitude criterion of 0.25 deg has been reported to exclude artefacts, while allowing detection for even small saccades (O'Driscoll et al., 2000), and preliminary analysis with the current data also showed that using no amplitude criteria included artefacts, while larger amplitudes excluded small saccades.

Measures

Dual-mode tracking: Dual-mode eye velocity (deg/s) and gain (eye velocity / target velocity) were measured to estimate visual tracking of combined smooth pursuit and saccadic eye movements.

Single-mode pursuit: Single-mode pursuit eye velocity (deg/s) and gain (eye velocity / target velocity) were measured to estimate smooth pursuit eye movements.

Saccades: Saccades were not classified into subcategories, as the focus of the study was to quantify and compare smooth pursuit and saccadic eye movements regardless of saccade type. Only square wave jerks (SWJs) were counted and analysed separately, as they have been well validated, and have clearly been established as an intrusive eye movement (Shaffer et al., 2003). They were defined as a pair of saccades in opposite directions, the first taking the eye off the target and the second refoveating (Leigh & Zee, 1999), with the two less than 400ms apart (Shaffer et al., 2003).

Measures to quantify saccadic eye movements: Four different measures were calculated from the total number of saccades for each target velocity:

Saccade frequency per second: This measure is obtained by dividing the number of saccades by the total tracking duration, and the saccade frequency index per second (per 1,000ms) is therefore a time-based frequency measure.

Saccade frequency per cycle: This measure is obtained by dividing the number of saccades by the number of tracking cycles, and the saccade frequency index per cycle (per 40.0 deg) is therefore a distance-based frequency measure.

Time-based saccade ratio: The total duration of saccadic eye movements for each velocity is divided by the total duration of smooth pursuit eye movements, providing

a time-based ratio measure of the time spent in saccadic versus smooth pursuit eye movements (Avila et al., 2003; Avila, Weiler et al., 2002).

Distance-based saccade ratio: The total amplitude of saccadic eye movements for each velocity is divided by the total amplitude of single-mode smooth pursuit, providing a distance-based ratio measure of the spatial distance covered by saccadic versus smooth pursuit eye movements (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999).

Saccade characteristics: Saccade amplitude (deg), duration (ms), and peak velocity (deg/s) were measured. Normal saccade amplitude and saccade peak velocity were compared with amplitude and peak velocity corrected for pursuit velocity (as per De Brouwer, Missal et al., 2002), using the following formulae:

*Saccade amplitude corrected = Saccade amplitude – (Saccade duration * Pursuit velocity)*

Saccade peak velocity corrected= Saccade peak velocity – Pursuit velocity

Data analysis

The data was initially analysed for effects of the direction of visual tracking, using separate 2 [Direction: Right, Left] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated measures ANOVAs for all dependent variables, apart from the saccade ratio data, which was calculated across tracking direction. All measures were then analysed for age and sex effects using a 2 [Sex: Female, Male] X 3 [Age Group: 18-24, 25-29, 30-39] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] mixed factor ANOVA. Separate 2 [Mode: Single, Dual] X 9 [Target Velocity: 2.5.0, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated

measures ANOVAs were conducted for eye velocity and gain, and repeated measures ANOVAs were used to compare saccade characteristics as a function of target velocity. Separate 2 [Ratio: Time-based, Distance-based] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated measures ANOVAs were also used to compare the two saccade frequency indices and the two saccade ratio measures. Greenhouse-Geisser corrections were applied to all within subjects variables with more than two levels and strict Bonferroni adjustments were used to adjust the alpha levels for all multiple comparisons. Significant interactions were followed up with individual ANOVAs. Significant main effects were followed up with pairwise comparisons, except for significant main effects of target velocity, which were followed-up using within-subjects contrasts because of the large number of values. Detailed statistical output files (using SPSS statistical software versions 14.0 and 16.0) are provided in electronic format in Appendices B-D.

Results

The effects of the direction of visual tracking

Separate 2 [Direction: Right, Left] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated measures ANOVAs were conducted to examine the effects of direction on visual tracking, and output files for these analyses are presented in Appendix B. Direction of tracking did not have a significant effect on any of the saccade characteristics, or on dual-mode tracking. For saccade frequency, there were significantly more saccades for right-to-left tracking than for left-to-right tracking [frequency per second: $F(1,21)=20.6$; $p<.001$, $\eta^2=.50$; frequency per cycle:

$F(1,28)=27.4$; $p<.001$, $\eta^2=.50$]. It is possible that this effect is due to the saccadic system being more used to rightward movements due to reading occurring in this direction. There was no difference in single-mode pursuit gain [$F(1,28)=3.3$; $p>.05$], but single-mode pursuit eye velocity was faster for right-to-left tracking than for rightward tracking [$F(1,28)=10.0$; $p<.01$, $\eta^2=.26$]. This effect is likely to be related to the larger number of saccades in the same direction. Eye velocity is briefly increased following a saccade during pursuit through post-saccadic enhancement (Gardner & Lisberger, 2001; Lisberger, 1998; Schoppik & Lisberger, 2006), and a greater number of saccades would therefore result in overall greater eye velocity. There were no significant interactions between the tracking direction and target velocity for any of the variables, indicating that the patterns for all variables as a function of target velocity are the same for left and rightward tracking, and all variables were therefore collapsed across tracking direction.

The effects of sex and age

Separate 2 [Sex: Female, Male] X 3 [Age Group: 18-24, 25-29, 30-39] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] mixed factor ANOVAs were conducted for each dependent variable, and the output files of these analyses are presented electronically in Appendix C.

There were no significant effects of Sex or Age on dual-mode tracking eye velocity [Sex: $F(1,23)=0.1$, $p>.05$; Age:$F(2,23)=0.9$, $p>.05$] and gain [Sex: $F(1,23)=0.5$, $p>.05$; Age: $F(2,23)=2.0$, $p>.05$], or on single-mode pursuit eye velocity [Sex: $F(1,23)=0.2$, $p>.05$; Age: $F(2,23)=1.9$, $p>.05$] and gain [Sex: $F(1,23)=0.0$, $p>.05$; Age: $F(2,23)=3.2$, $p>.05$]. Sex and Age also had no effect on saccade frequency per

second and per cycle [Sex: $F(1,23)=1.9$, $p>.05$; Age: $F(2,23)=0.1$, $p>.05$], or the time-based [Sex: $F(1,23)=3.5$, $p>.05$; Age: $F(2,23)=0.7$, $p>.05$] and distance-based [Sex: $F(1,23)=0.8$, $p>.05$; Age: $F(2,23)=0.6$, $p>.05$] saccade ratio measures. However, a three-way interaction of Sex, Age and Target Velocity was consistently found for all characteristics of saccadic eye movements, including saccade amplitude [$F(5,58)=3.3$, $p<.025$, $\eta^2=.22$], corrected amplitude [$F(5,1)=2.9$, $p<.05$, $\eta^2=.21$], saccade duration [$F(8,86)=2.1$, $p=.05$, $\eta^2=.15$], saccade peak velocity [$F(8, 92)=3.0$, $p<.01$, $\eta^2=.21$] and corrected peak velocity [$F(9,106)=2.4$, $p<.025$, $\eta^2=.17$]. These significant three-way interactions were further followed up with individual ANOVAs for each age group, and this consistently revealed an interaction of Sex and Target Velocity only for the 25-29 year old observers ($p<.016$). As illustrated in Figure 7, at fast target velocities (faster than 25.0 deg/s), females tended to make larger and faster saccades than males.

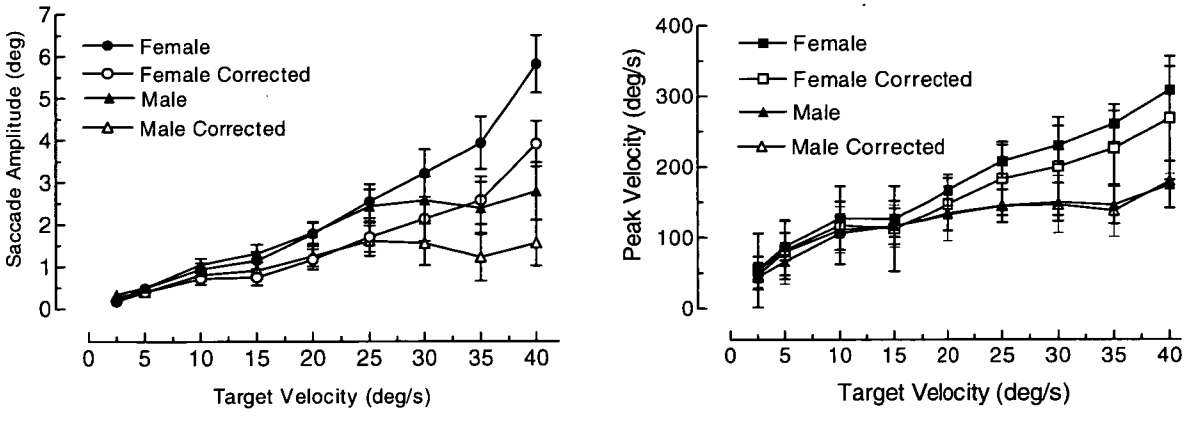

Figure 7. Interaction between Sex and Target Velocity for the 25-29 year age group (error bars depict standard error of the means, *SE*) for saccade amplitude and peak velocity (normal and corrected for peak velocity).

For the peak velocity variables (with and without corrections), there was also an interaction between Age and Target Velocity [peak velocity: $F(8, 92)=3.0$, $p<.01$, $\eta^2=.21$, corrected peak velocity: $F(9,106)=4.2$, $p<.001$, $\eta^2=.27$]. Follow-up ANOVAs showed that there were no age effects at target velocities up to 15.0 deg/s, but at faster velocities the middle age group (25-29 years) had significantly faster saccade peak velocity than the other two groups ($p<.016$). All age and sex effects had very small effect sizes, suggesting that although statistically significant, they may not be very meaningful, and the data was therefore collapsed across sex and age for all further analyses.

The effects of target velocity

The means and standard deviations for all 14 measures at each of the nine target velocities are presented in Table 1, and the statistical output files for these analyses are presented in electronic format in Appendix D.

Table 1. Means and standard deviations (in brackets) for dual-mode tracking and single-mode pursuit and saccade variables at each target speed

Target Velocity (deg/s)	2.5	5.0	10.0	15.0	20.0	25.0	30.0	35.0	40.0
Dual-Mode Tracking									
Dual-Mode Eye Velocity (deg/s)	2.24(0.2)	4.37(0.5)	9.19(1.2)	13.32(2.1)	17.97(2.9)	21.83(4.7)	23.67(7.0)	25.70(8.8)	28.94(12.6)
Dual-Mode Tracking Gain	0.90(0.1)	0.88(0.1)	0.92(0.1)	0.89(0.1)	0.90(0.1)	0.87(0.2)	0.80(0.2)	0.73(0.3)	0.72(0.3)
Single-Mode Pursuit									
Single-Mode Eye Velocity (deg/s)	2.19(0.9)	3.73(0.7)	7.81(1.5)	11.42(2.2)	14.90(2.9)	17.96(4.5)	19.61(7.4)	21.57(7.7)	22.20(9.6)
Single-Mode Pursuit Gain	0.88(0.4)	0.75(0.2)	0.78(0.2)	0.76(0.1)	0.75(0.1)	0.72(0.2)	0.65(0.2)	0.62(0.2)	0.56(0.2)
Saccade Measures									
Saccade Frequency Index Per Second	0.67(0.5)	1.11(0.7)	2.07(1.1)	3.14(1.3)	4.2(1.9)	4.98(2.3)	5.02(2.0)	5.57(2.0)	5.83(2.2)
Saccade Frequency Index Per Cycle	5.07(3.4)	4.73(2.4)	4.79(2.0)	4.85(2.2)	4.55(2.1)	3.82(1.5)	3.64(1.3)	3.33(1.3)	1.45(1.0)
Time-based Ratio of Saccades	0.010(0.0)	0.02(0.0)	0.03(0.0)	0.07(0.0)	0.11(0.1)	0.16(0.1)	0.21(0.1)	0.28(0.1)	0.37(0.1)
Distance-based Ratio of Saccades	0.14(0.2)	0.15(0.1)	0.22(0.2)	0.34(0.2)	0.53(0.4)	0.78(0.7)	1.24(1.3)	1.51(1.6)	2.36(2.9)
Saccade Duration (ms)	18(3.6)	19(3.9)	23(4.7)	26(5.6)	29(5.8)	31(6.0)	35(7.1)	35(7.0)	38(9.8)
Saccade Amplitude (deg)	0.36(0.2)	0.55(0.2)	1.00(0.3)	1.33(0.5)	1.73(0.6)	2.20(0.9)	2.82(1.2)	3.20(1.5)	3.81(1.9)
Saccade Amplitude Corrected (deg)	0.32(0.2)	0.46(0.2)	0.77(0.3)	0.93(0.4)	1.16(0.5)	1.42(0.8)	1.77(1.1)	1.97(1.3)	2.37(1.5)
Saccade Peak Velocity (ms)	62.85(30.8)	83.22(33.7)	115.11(37.9)	130.23(40.7)	139.01(38.0)	152.79(48.2)	170.52(55.5)	186.57(60.6)	208.48(73.9)
Saccade Peak Velocity Corrected (ms)	61.63(30.1)	81.84(33.2)	107.63(34.8)	118.03(36.5)	123.46(33.1)	132.10(44.9)	145.46(53.0)	156.25(54.6)	179.00(63.0)
Number of SWJs (per cycle)	1.11(1.4)	0.53(0.7)	0.25(0.4)	0.13(0.3)	0.02(0.1)	0.01(0.1)	0.01(0.1)	0.00(0.0)	0.00(0.0)

N=29

Dual-mode tracking and single-mode pursuit

Eye velocity for dual-mode tracking was significantly faster than for single-mode pursuit [$F(1,28)=25.2$, $p<.001$ $\eta^2=.47$], demonstrating that there is a significant saccadic component to the overall tracking response. Also, as expected, eye velocity increased significantly with increasing target velocity [$F(1,40)=137.0$, $p<.001$ $\eta^2=.83$], with the eyes speeding up to keep up with the target. There was also a significant interaction between the mode of tracking (dual- vs. single-mode) and target velocity on eye velocity [$F(2,50)=7.3$, $p<.01$ $\eta^2=.21$], which was followed up with paired-sample t-tests at each target velocity (with Bonferroni-adjusted $\alpha=.006$). The results revealed that single- and dual-mode eye velocity did not differ significantly at 2.5 deg/s target speed, but for all faster target speeds eye velocity for dual-mode tracking was significantly faster than for single-mode pursuit alone. Also, as illustrated in Figure 8, the difference between single- and dual-mode tracking became more pronounced with increasing target speed.

Dual-mode tracking gain was also significantly higher than single-mode pursuit gain, [$F(1,28)=35.4$, $p<.001$, $\eta^2=.56$], and gain for both single-and dual-mode tracking significantly decreased with increasing target velocity [$F(2,67)=11.6$, $p<.001$, $\eta^2=.29$]. There was no significant interaction between the mode of tracking and target velocity [$F(3,71)=1.9$, $p>.10$, $\eta^2=.06$] (see Figure 8), indicating that dual-mode tracking, which combines both smooth pursuit and saccadic eye movements, was superior to single-mode pursuit alone. This reveals that saccadic eye movements contribute to overall visual tracking even at very slow target velocities (2.5, 5.0 deg/s).

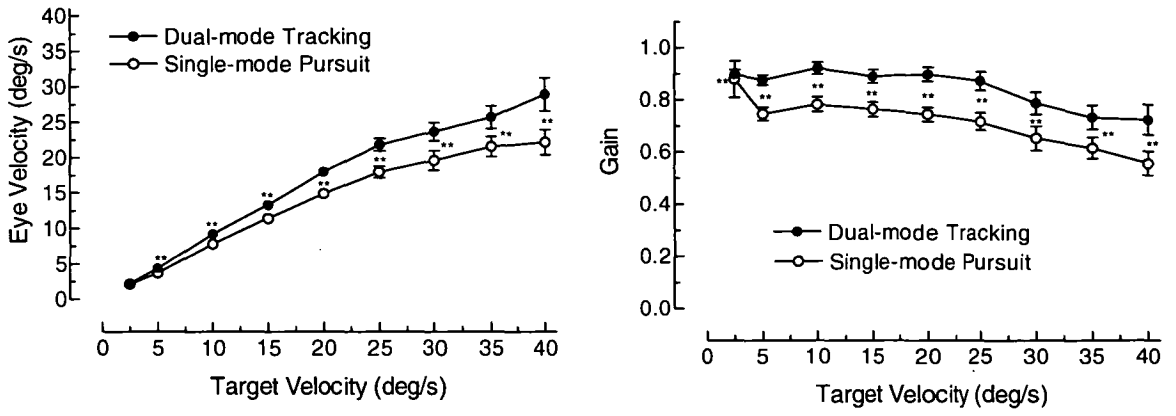

Figure 8. Eye velocity and gain for dual-mode tracking and single-mode pursuit. ** indicate significant differences ($p<.001$); error bars denote *SE*. Eye velocity best fitted a linear trend for both dual-mode tracking [$F(1,28)=165.2$, $p<.001$, $\eta^2=.86$] and single-mode pursuit [$F(1,28)=143.4$, $p<.001$, $\eta^2=.84$]. Dual-mode tracking gain [$F(1,28)=10.2$, $p<.01$, $\eta^2=.27$] and single-mode pursuit gain [$F(1,28)=18.0$, $p<.001$, $\eta^2=.39$] both decreased linearly.

Saccade frequency

Comparing the two saccade frequency indices using a 2 [Index: Per second, Per cycle] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated measures ANOVA revealed significant effects of Frequency Index [$F(1,28)=18.0$, $p<.001$, $\eta^2=.39$] and Target Velocity [$F(3,87)=12.74$, $p<.001$, $\eta^2=.31$]. The number of saccades made per cycle was significantly larger than the number of saccades per second, but this is not surprising given that a 40.0 deg tracking cycle can be of very long duration, ranging from 1,000 to 16,000 ms. Interestingly, there was a significant interaction between the type of saccade frequency measure and target velocity [$F(4,115)=74.6$, $p<.001$, $\eta^2=.73$], and the two frequency indices exhibited vastly different patterns as a function of velocity, as illustrated in Figure 9. With increasing target speed, significantly more saccades were generated per second, in contrast to the significant decrease in the number of saccades per cycle (per 40.0 deg spatial

distance). This shows that these two measures deliver fundamentally different results when used with more than one target velocity.

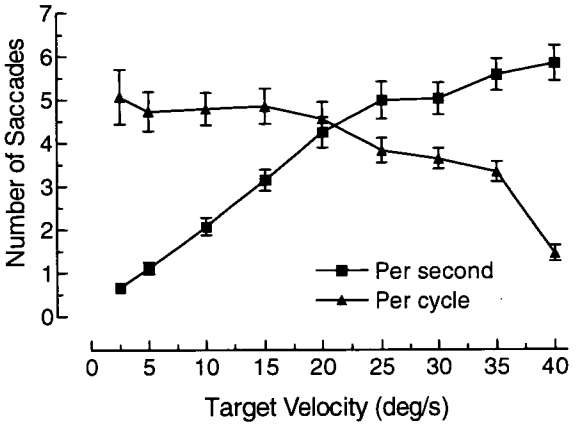

Figure 9. Mean saccade frequency per second and per cycle as a function of target velocity (error bars depict *SE*). Saccade frequency per second increased linearly [$F(1,28)=207.4$, $p<.001$,$\eta^2=.88$], while the number of saccades per cycles decreased linearly [$F(1,28)=8.6$, $p<.001$,$\eta^2=.23$].

Saccade characteristics

The saccade main sequence of saccade duration versus saccade amplitude is displayed for both normal and corrected amplitude in Figure 10. The linear main sequence relationship is evident for both measures, although the linear fit is better when amplitude is not corrected, because no correction is applied to saccade duration.

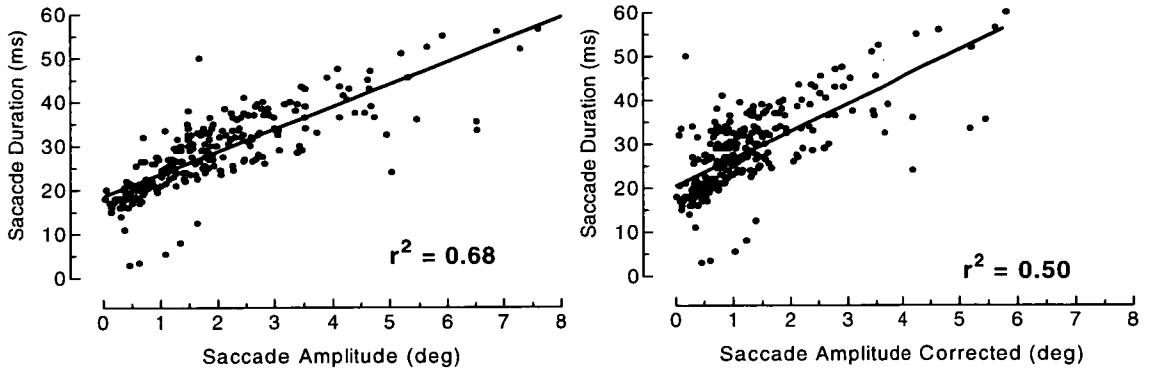

Figure 10. Main sequence relationship between mean saccade amplitude (normal and corrected) and mean saccade duration for all saccades generated in the tracking of continuous motion.

The main sequence relationship between peak velocity and saccade amplitude also follows the proposed main sequence relationship, as displayed in Figure 11 for both normal and corrected values. The graphs illustrate that when both measures are corrected for pursuit velocity, there is less variability, and the pattern follows more closely that of saccades to stationary targets (De Brouwer, Missal et al., 2002).

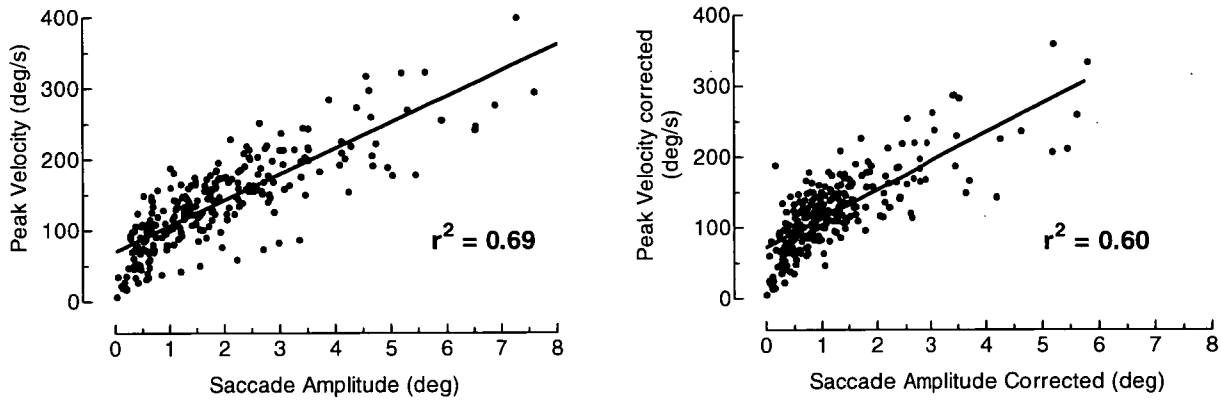

Figure 11. Main sequence relationship between mean saccade amplitude and mean saccade peak velocity (both normal and corrected) for all saccades generated in the tracking of continuous motion.

As summarised in Table 2 and Figure 12, a significant linear increase with increasing target velocity was evident for all saccade characteristics. With increasing target velocity, saccades became increasingly larger, faster and of longer duration.

Table 2. Main effects and linear trends of saccade variables as a function of target velocity.

Saccade Variable	Main Effect Velocity	Linear Trend
Amplitude	$F(2,59)=65.0$, $\eta^2=.70$	$F(1,28)=128.1$, $\eta^2=.82$
Amplitude (corrected)	$F(2,65)=30.6$, $\eta^2=.52$	$F(1,28)=61.1$, $\eta^2=.68$
Duration	$F(3,85)=83.9$, $\eta^2=.75$	$F(1,28)=185.9$, $\eta^2=.87$
Peak Velocity	$F(3,81)=51.6$, $\eta^2=.65$	$F(1,28)=105.3$, $\eta^2=.79$
Peak Velocity (corrected)	$F(3,90)=34.8$, $\eta^2=.55$	$F(1,28)=74.2$, $\eta^2=.73$

This increase in the magnitude of saccade characteristics as a function of target velocity was evident even when saccade amplitude and peak velocity were corrected for pursuit velocity, which suggests that these findings are not caused by an increase in pursuit eye velocity, but reflect real changes in the dynamics of the saccades themselves. Direct comparisons (using ANOVAs followed by Bonferroni-adjusted pairwise comparisons) showed that applying these corrections had a significant effect on saccade amplitude and peak velocity. The corrections resulted in a significant decrease in saccade amplitude at all target velocities, and also reduced saccade peak velocity for target speeds above 5.0 deg/s, and this effect was more pronounced for fast pursuit velocities, consistent with the formula.

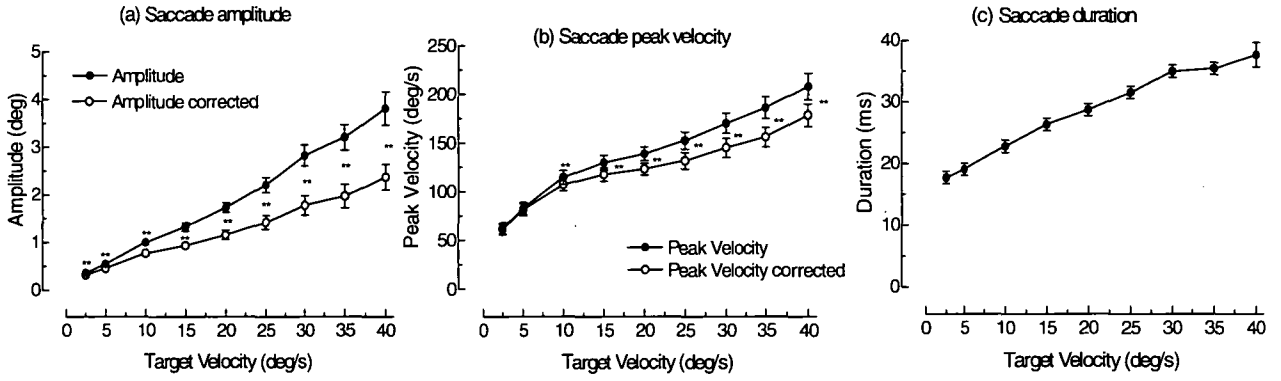

Figure 12. Linear increase of (a) saccade amplitude (with and without corrections), (b) saccade peak velocity (with and without corrections), and (c) saccade duration with increasing target velocities. * denote significant differences between the measures with and without corrections ($p<.005$); error bars depict *SE*.

Ratio of saccadic versus smooth pursuit eye movements

The two ratio measures of saccadic versus pursuit eye movements were compared using a 2 [Ratio Measure: time-based, distance-based] X 9 [Target Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0, 40.0] repeated measures ANOVA. This revealed significant effects of Ratio Measure [$F(1,28)=26.5$, $p<.001$, $\eta^2=.49$] and Target

Velocity [$F(1,40)=20.0$, $p<.001$, $\eta^2=.42$], but also a significant interaction between the type of ratio and target velocity [$F(1,37)=35.5$, $p<.01$, $\eta^2=.29$]. As illustrated in Figure 13, separate ANOVAs for each measure indicated that both the time-based [$F(3,73)=125.0$, $p<.001$, $\eta^2=.82$] and the distance-based ratio measure [$F(1,38)=15.4$, $p<.001$, $\eta^2=.36$] demonstrate an increasingly larger saccadic tracking contribution with increasing target velocity (see Figure 13), but the distance-based ratio of saccadic eye movements increased more strongly than the time-base ratio.

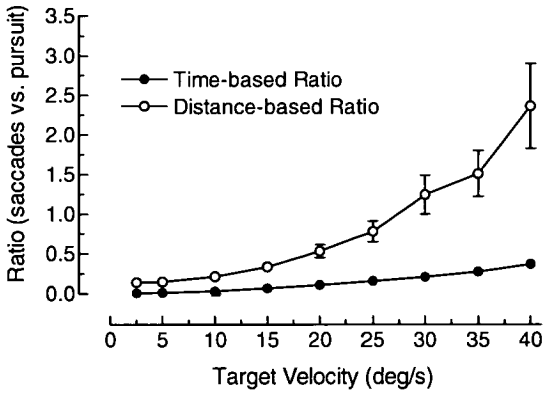

Figure 13. Time-based and distance-based ratios of saccadic versus smooth pursuit eye movements (error bars depict SE). A linear trend best fitted saccadic ratio of time [$F(1,28)=390.1$, $p<.001$, $\eta^2=.93$], and spatial distance [$F(1,28)=22.0$, $p<.001$, $\eta^2=.44$].

The relative contribution of saccades to dual-mode tracking therefore differs considerably depending on whether their contribution is estimated based on time or distance. The time-based ratio of saccades (i.e., time spent in saccadic versus smooth pursuit eye movements) is rather small, and even at the fastest target speed (40.0 deg/s) smooth pursuit eye movements make up the main proportion of visual tracking, with a 2:3 ratio of saccadic versus smooth pursuit eye movements. The distance-based ratio of saccades (i.e., distance covered by saccadic versus smooth pursuit eye movements) is significantly larger, with a large proportion of the spatial

trajectory covered by saccades, especially at faster target speeds. A 1:1 ratio of saccades versus smooth pursuit is reached at target speeds above 20.0 deg/s and saccades cover more than twice the distance compared with smooth pursuit at 40.0 deg/s.

Frequency of square-wave jerks (SWJs)

SWJs were counted separately and the mean number of SWJs per cycle was presented in Table 1. A repeated measures ANOVA revealed that the number of SWJs made per 40.0 deg-cycle decreased with increasing target velocity [$F(1.3,35)=15.4$, $p<.001$, $\eta^2=.36$]. Within subjects' contrasts showed a cubic trend [$F(1,28)=10.1$, $p<.01$, $\eta^2=.27$], reflecting the sharp decrease from 2.5 to10.0 deg/s and the more gentle decrease to zero from 10.0 to 20.0 deg/s target speed. Looking at the raw data confirmed that no SWJs were made by any participant for target speeds above 20.0 deg/s. This decrease in the rate of SWJs with increasing target velocity has been reported previously (Shaffer et al., 2003), and suggests that these intrusive eye movements are a phenomenon associated with visual tracking at slow target speeds.

Discussion

Summary of the main findings

The present study revealed a number of important findings:

1. The only effects for sex and age were found for saccade characteristics, females in the 25-29 year old age-group generating significantly larger and faster saccades at target velocities exceeding 25.0 deg/s.

2. There was a linear decrease in both dual-mode tracking and single-mode pursuit gain with increasing target velocity, but dual-mode tracking gain was significantly better than single-mode gain at all target velocities.
3. The number of saccades generated per second increased as a function of target velocity, but the number of saccades per cycle of tracking decreased with increasing target speed.
4. There was a significant saccadic contribution to visual tracking at all target velocities, which is supported by a significant linear increase of both time-based and distance-based ratio measures of saccadic versus pursuit eye movements with increasing target velocity. At the fastest target velocity (40.0 deg/s) saccadic eye movements covered more than twice the spatial distance compared with smooth pursuit, and this is consistent with the parallel increase in saccade amplitude, duration and peak velocity.

The effects of sex and age

The findings showed that there were no differences between males and females with regard to dual-mode tracking, single-mode pursuit or in the number of saccades made during visual tracking. Also, no age effects were found for the examined age range for dual-mode tracking, single-mode pursuit or saccade frequency, which suggests that visual tracking is largely unaffected by age in the range of 18-39 years, consistent with similar findings for saccadic eye movements (Irving et al., 2006). Only some of the saccade characteristics were affected by the sex and age of the observer, although effects sizes were very small, with less than 30% of the variance due to sex or age. Females in the 25-29 year age group produced significantly larger and faster saccades than males, but only at velocities exceeding 25.0 deg/s. It is possible that these effects

are due to a larger variability if noise levels in this age group, but this cannot be tested by the current apparatus. If the current results reflect a real sex effect, the possibility that sex differences may be dependent on target velocity could explain the mixed findings in the literature, as existing studies have used a range of different velocities. Kelly and Bakan (1999) examined visual tracking at fast velocities (24.0 and 48.0 deg/s) and found that females had better visual tracking, whereas studies that have found better tracking in males have used target velocities of 20.0 deg/s and below (T. J. Hutton et al., 1983; Kuechenmeister et al., 1977) and have only found sex differences in older observers. The sex differences in the current study were restricted to the 25-29 year age-group, and this group also exhibited faster saccade peak-velocity than the other groups, a finding that cannot be readily explained, and it is possible that this is due to the relatively small sample sizes for males and females in each age group. Sex differences in visual tracking certainly require further investigation with greater sample sizes, and based on the current findings it is recommended that in future studies sex differences are examined at a range of target velocities, including both slow and fast target speeds.

Dual-mode tracking and single-mode pursuit

Dual-mode tracking gain decreased linearly but gently as a function of stimulus velocity, but remained at generally high levels even at fast target velocities. This is consistent with values in early studies that did not separate the saccadic and smooth pursuit tracking components (e.g., Schalen, 1980; Sharpe & Sylvester, 1978). Absolute values of single-mode pursuit gain were rather low, but they were still within what is generally considered the normal range (Pola, 2002). Single-mode pursuit gain did not exceed 0.8 even at the slowest target velocities and decreased

linearly to below 0.6 at the fastest target speeds. There are several reasons for the rather low smooth pursuit gain in the current study: the stimulus was very small (2.5 deg), and covered a large trajectory amplitude (20.0 deg), which have both been shown to affect smooth pursuit performance (Leigh & Zee, 1999), and observers were unpractised.

Single-mode pursuit gain was highest at slow target velocities and decreased significantly and linearly with increasing target velocity, consistent with what was expected based on the literature. This decrease in single-mode pursuit gain is a result of the target velocity exceeding the optimal velocity range of the pursuit system, causing the eye to lag behind the target (Lisberger et al., 1987). In relation to a lower velocity limit for smooth pursuit, if there is such a lower velocity threshold at which single-mode gain deteriorates, it is below a stimulus velocity of 2.5 deg/s for a single-dot target, because no deterioration of single-mode pursuit gain was found for the target velocities examined in this study. Murphy (1978) found inconsistent results for single-mode pursuit performance at target speeds just below 1.0 deg/s, while Churchland and Lisberger (2000) had to discard dual-mode tracking data for apparent motion stimuli below 2.0 deg/s, because they found it to be too variable and to contain too many saccades. Velocities of 1.0-2.0 deg/s have also been found to be associated with slower pursuit acceleration and significantly higher latencies, as well as larger position errors and lower gain (Carl & Gellman, 1987; Spering et al., 2005). These findings suggest that single-mode pursuit eye movements may deteriorate at very slow target speeds, but any further investigation of this with a small single dot target needs to include target velocities below 2.5 deg/s. Furthermore, the significant and consistent differences found between dual-mode tracking and single-mode

pursuit demonstrate that smooth pursuit eye movements do not track the target alone, but that saccadic eye movements make a significant tracking contribution at all target velocities, and this is supported by the saccade frequency and saccade ratio data.

Saccade frequency

The two measures of saccade frequency exhibited dramatically different patterns as a function of target velocity, which demonstrates the significance of the choice of saccade frequency measure when investigating visual tracking, as well as the importance of specifying which measure is reported. This is particularly relevant when quantifying the frequency of specific types of saccades (e.g., anticipatory or catch-up saccades), or in the investigation of disordered visual tracking, such as in observers with schizophrenia, in whom the number of saccades is a central measure of disordered tracking (see Chapter 4). The number of saccades generated per second follow the hypothesised pattern, with an increase in saccade frequency associated with increasing target velocity. This finding is consistent with the simultaneous decrease in single-mode pursuit gain, in line with the notion that saccades during visual tracking are a direct result of the increased position error due to the eye increasingly lagging behind the target. In contrast, saccade frequency per cycle (per 40.0 deg spatial trajectory) shows the opposite pattern, with significantly more saccades generated per cycle at slow target speeds than at faster stimulus velocities. Saccade frequency per cycle represents the number of saccades per spatial distance and this measure is therefore similar to the popular measure of absolute saccade frequency, which specifies the number of saccades present during the total number of tracking cycles. It can be expected that more saccades per cycle are produced at slower target velocities, given that significantly more time is necessary to cross a

given trajectory when the target moves more slowly, but this increase in crossing time cannot be the only explanation for this finding. For example, the time necessary to cross the trajectory is cut in half when target speed increases from 2.5 to 5.0 deg/s and from 5.0 to 10 deg/s target velocity, with only a very small associated decrease in the number of saccades per cycle, but a similar halving of the overall tracking time from 20.0 to 40.0 deg/s target velocity results in a substantial decrease in saccade frequency per cycle. Saccade frequency per cycle therefore reflects a real decrease in the number of saccades generated to cross the spatial trajectory at faster target velocities. In contrast, the number of saccade per second doubles every time the time taken to cross the trajectory is cut in half, which contributes to its fairly linear increase with increasing target velocity, and suggests that this increase is probably more strongly related to crossing time. Such stark differences in patterns strongly suggests that one or even both measures are flawed when more than one target velocity is used, at least if they are interpreted in isolation. At a range of different target speeds, the spatial trajectory remains the same while the time required to cross it varies significantly, and of the two frequency measures, the distance-based saccade frequency index (i.e. number of saccades per cycle or per degree) is therefore more valid for studies examining more than one target speed. Nevertheless, neither measure takes into account saccade characteristics, which means that they are both limited with regard to measuring the real saccadic contribution to dual-mode tracking.

Saccades characteristics

Because the saccade frequency measures do not take into account saccade dynamics they should always be interpreted in conjunction with measures of saccade characteristics. The main sequence relationships for saccadic eye movements

generated during visual tracking were highly similar to the patterns reported for saccades generated to both stationary and moving targets (e.g., De Brouwer, Missal et al., 2002), and this supports the view that the mechanisms underlying saccadic eye movements in response to stationary and moving stimuli are very similar (Kimmig et al., 2002; Krauzlis & Miles, 1996b).

As expected, saccades were increasingly larger, faster, and of longer duration with increasing target velocity, and this pattern was evident even after the pursuit velocity component was removed from saccade amplitude and peak velocity (as in De Brouwer, Missal et al., 2002). This shows that these increases in magnitude of saccade characteristics at faster target velocities reflect real changes in the saccade dynamics associated with faster stimulus velocities, and are not merely the result of the smooth pursuit response added to the saccades. However, effect sizes for velocity effects were smaller after the correction was applied, which demonstrates that the corrected variables are the more stringent measures, because any variability due to smooth pursuit eye movements is removed from the saccade characteristics. Applying these corrections therefore allows the detection of purer effects of stimulus velocity on saccade characteristics, and they are therefore recommended when investigating saccade characteristics, particularly when different target speeds are used or saccades to stationary and moving stimuli are compared. De Brouwer and colleagues (De Brouwer, Missal et al., 2002) did not apply a correction to saccade duration, because they compared saccade amplitude and saccade peak velocity for saccades of equal duration. Saccade duration is likely to be similarly affected by pursuit dynamics, and a similar correction may need to be considered for saccade duration in the future,

although these effects would be expected to be very small given the rapid acceleration of the eye during saccades.

The findings relating to saccade characteristics in combination with the saccade frequency data suggest that at slower target velocities, the saccadic component to visual tracking consists of a large number of smaller, briefer and slower saccades crossing a given spatial trajectory. With increasing target velocity, saccades become larger, faster and of longer duration, and because they are larger, fewer saccades are necessary to cover the spatial distance. Because the time taken to cross the spatial trajectory is much shorter at faster velocities, the number of saccades per second still increases with increasing target velocity. The finding of a large number of small saccades at slow target velocity and a small number of large saccades at fast target velocities is consistent with previous reports that the position errors triggering saccades varies depending on target speed. Collewjin and Tamminga (1984) found that small position errors of 0.2 deg/s elicited corrective saccade at slow tracking speeds, while at faster velocities larger position errors were required (e.g., 1.3 deg). Also, small position errors have been found to be generally tolerated without triggering a saccade at moderate to fast velocities (Collewijn & Tamminga, 1984: up to 0.5 deg; Gellman & Carl, 1991: up to 0.1-0.2 deg).

Ratio of saccadic versus smooth pursuit eye movements

In contrast to the saccade frequency measures, the measures of saccade ratio combine information about saccade frequency and saccade characteristics. According to Ross and colleagues (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999;

Randal G. Ross et al., 1999), reporting a distance-based ratio of saccadic eye movements has clear advantages over a simple frequency index, as they incorporate information about saccade amplitude. Subsequent studies (Avila et al., 2003; Avila, Weiler et al., 2002) have reported a time-based ratio measure of the time spent in saccadic versus smooth pursuit eye movements, stating that this was similar to the distance-based measure used by Ross and colleagues. The current results, however, show that this is not the case and that time-based and distance-based ratio measures of saccadic versus pursuit eye movements deliver rather different findings. Even though in the present study both ratio measures showed an increase in the saccadic contribution to dual-mode tracking with increasing target velocity, there are large differences between the time-based and distance-based ratio measures. The time-based measure (Avila et al., 2003; Avila, Weiler et al., 2002) underestimates the true contribution of the saccadic system to dual-mode tracking for the following reasons. First, the time-based ratio measure is affected by both saccade duration and peak velocity. When saccades become larger at faster target velocities their duration increases, but they also become faster, which in turn reduces the relative time spent in saccadic eye movements. Second, smooth pursuit eye movements are naturally much slower than saccadic eye movements, and this means that, by default, a significantly larger amount of time is spent in smooth pursuit than in saccadic eye movements, which does not reflect the actual extent of the saccadic contribution to dual-mode tracking. For example, the time-based ratio measure would only show a small saccadic contribution even when the saccadic tracking component is quite substantial, because saccades are much faster and of shorter duration than smooth pursuit eye movements, particularly at fast stimulus velocities. Finally, smooth pursuit eye movements become faster at faster target velocities, and the overall time spent in

pursuit eye movements therefore decreases with increasing target speed, which results in an increase in the time-based ratio of saccades versus pursuit that does not reflect an actual change in the contribution of the two types of eye movements to dual-mode tracking. Hence, time-based ratio measures are affected by numerous confounding variables and are therefore not a valid way of estimating the saccadic component of visual tracking.

Unlike time-based measures, distance-based measures of the saccadic contribution to visual tracking only consider the spatial trajectories covered by each eye movement, and they are therefore unaffected by temporal variables, which makes the estimation of the saccadic contribution to dual-mode tracking in terms of spatial distance a more objective and valid measure. Also, in contrast to the distance-based saccade frequency index (i.e., saccade frequency per cycle), the ratio of spatial distance covered by saccades versus pursuit is not affected by the overall tracking time, and is therefore independent of target velocity, which makes it also superior to saccade frequency per cycle in estimating the saccadic tracking component. It is therefore concluded that the distance-based ratio measure is the only measure of saccadic contribution to visual tracking that is unaffected by target velocity, temporal variables, or the inherent dynamics of saccadic and pursuit eye movements. This measure, which was first used by Ross and colleagues (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999), is therefore the preferable measure to quantify the saccadic tracking component, and this is particularly important when more than one target speed is measured.

Frequency of square-wave jerks

The number of square-wave jerks decreased with increasing target velocity and no square-wave jerks were made by any participant once target velocity exceeded 20.0 deg/s. This suggests that these intrusive eye movements are a phenomenon associated with visual tracking at slow target speeds. Shaffer, Krisky, and Sweeney (2003) reported that increasing task demands during visual tracking, such as lowering target predictability or increasing target velocity, significantly lowered the frequency of square-wave jerks. Because the initial intrusive saccade of square-wave jerks are believed to be a lapse in inhibitory control in the brain stem (Leigh & Zee, 1999), Shaffer, Krisky, and Sweeney (2003) suggested that increasing task demands may influence the top-down modulation of the brain stem, which improves inhibitory control and therefore reduces the number of intrusive saccades. It is therefore recommended that square-wave jerks are removed from analyses of saccades during visual tracking, especially when both slow and fast target velocities are examined, so they do not contaminate the analysis of saccadic eye movements at slow target speeds or the comparison of saccades at different stimulus velocities.

Summary and conclusions

In combination, the findings of Experiment 1 relating to both smooth pursuit and saccadic tracking components suggest that saccadic eye movements make a significant contribution to dual-mode tracking at all target velocities. This is evidenced by significant differences between dual-mode tracking gain and single-mode pursuit gain at all target velocities. At slow target velocities, smooth pursuit eye movements complete the majority of the tracking response, in terms of both time and distance, while saccades supplement smooth pursuit by way of a number of small

saccades, which are triggered by small but frequent position errors (Collewijn & Tamminga, 1984), as well as the retinal velocity signal (Blohm et al., 2003; De Brouwer, Missal et al., 2002; De Brouwer et al., 2001; De Brouwer, Yuksel et al., 2002; Gellman & Carl, 1991; Keller & Johnsen, 1990; Kim et al., 1997; Ron et al., 1989b; Schreiber et al., 2006). With increasing target velocity, the contribution of saccadic eye movements increases, and a smaller number of larger and faster saccades of longer duration are generated, triggered mostly by the large retinal position errors caused by the eye lagging behind the target, while taking into account the retinal velocity signal. In the current study, these large saccades covered the majority of the spatial trajectory when target velocity exceeded 20.0 deg/s and dual-mode tracking therefore consisted mainly of saccadic eye movements at these fast target speeds.

Even though the saccadic contribution does increase with increasing target velocity, the notion that the saccadic system just aids the pursuit system at fast velocities due to the eye lagging behind the target may be too simplistic an explanation. The current findings suggests that the full picture of the interplay between saccadic and smooth pursuit eye movements during visual tracking may be more complex, in terms of changing combinations of saccade frequency and characteristics produced at slow and fast target velocities. In this context, the use of apparent motion paradigms may provide further insight into the temporal and spatial aspects of visual tracking in order to tease out the relative roles of the saccadic and smooth pursuit tracking components.

Chapter 7

The saccadic and smooth pursuit components of visual tracking of apparent visual motion stimuli (Experiment 2)

The use of continuous motion is an important and necessary part of studying visual tracking and it has increased our understanding of single-mode pursuit eye movements. As outlined in Chapter 4, the use of apparent motion paradigms has provided a number of advantages over continuous motion and research employing these stimuli has provided insight into the mechanisms underlying motion perception during the previous century. A major advantage of apparent motion stimuli is that they allow the systematic degrading of the motion stimulus into its spatial and temporal components and into separate position and velocity signals. This allows the investigation of the effects of the different components of the motion signal on visual tracking. Apparent motion paradigms have also provided some insight into the nature of disordered visual tracking in schizophrenia, an important area of research in understanding the nature of schizophrenia and its diagnosis. For example, Slaghuis, Hawkes, Holthouse, and Bruno (2007a) showed that the visual tracking deficit was found more consistently when apparent motion stimuli were used and they also succeeded in inducing disordered smooth pursuit eye movements in normal observers.

Despite these advantages, apparent motion has not yet been used extensively in the study of eye movements, and the few studies that have done so vary greatly with regard to the types of apparent motion stimuli that have been used. A specific apparent motion paradigm called *sigma motion* (Behrens & Grüsser, 1979; Heywood,

1973; Lamontagne, 1973; Stoper, 1967, cited in Bridgeman, Mayer, & Glenn, 1976; see Chapter 4) is rather complex, as it depends on the actual movements of the eyes, and it has been used more commonly to study optokinetic eye movements (e.g., D. Adler et al., 1981; Flandrin et al., 1990). Apparent motion paradigms based on actual discrete target displacements (beta movement) are better suited to investigating visual tracking, because they are more closely related to naturally occurring events, and such apparent motion stimuli were first used by Hansel (1953) and Westheimer (1954) to study visual tracking. There are only very few studies that have since applied this type of apparent motion to visual tracking research, despite their frequent use in research of visual motion perception. Some experiments have used successively presented *stationary* stimuli to elicit eye movements (Barnes et al., 1987; M. M. Churchland & Lisberger, 2000; Morgan & Turnbull, 1978; Slaghuis et al., 2007a), and this has been called the *jumping-dot* paradigm (Slaghuis et al., 2007a). Other studies have used intermittent presentations of a *moving* stimulus (Barnes & Asselman, 1992; Hansel, 1953; Westheimer, 1954), generating a kind of *slashed motion.* Even though both apparent motion stimuli can result in the perception of apparent motion, the two are not identical. Jumping-dot apparent motion stimuli provide only retinal position information (through retinal image displacement), because they do not contain an actual retinal velocity signal. In contrast, slashed motion stimuli provide both position and velocity information, because they contain a retinal velocity signal. Therefore, by directly comparing the two apparent motion stimuli it is possible to separate out and investigate the different contributions of position and velocity signals in evoking visual tracking eye movements. In addition, by investigating both single-mode pursuit and saccadic tracking components, it may also be possible to determine if position and velocity signals differentially affect the

two eye movement systems. Visual tracking elicited with the use of jumping-dot and slashed motion has never been directly compared. Very brief presentations of a slashed motion stimulus have been presented as a position information-only control (Barnes & Asselman, 1992), because target exposure is believed to be too brief for the visual system to elicit any velocity information. In contrast, the present study directly compares the two types of apparent motion stimuli under identical stimulus conditions, which allows for a more direct and valid evaluation of the two.

Furthermore, as described in Chapter 4, previous studies of visual tracking of apparent motion have varied greatly with regard to the spatial and temporal parameters and the target velocities investigated. For example, Barnes and colleagues examined the effects of varying stimulus duration of each target presentation from 10-320ms, in separate studies for jumping-dot (Barnes et al., 1987) and slashed motion (Barnes & Asselman, 1992). For jumping-dot apparent motion stimuli, a decrease in single-mode pursuit performance was evident with increasing stimulus duration, while slashed motion stimuli produced the opposite effect, with increased pursuit performance associated with increasing stimulus duration. Barnes and Asselman (1992) concluded that for stimulus durations exceeding 30ms, the motion signal available to the visual system 'synergistically' increases eye velocity during target presentation, while a stationary target 'antagonistically' slows eye velocity (p.635), but this has not yet been examined directly under identical experimental conditions.

With regard to the target separation for apparent motion stimuli, some studies have investigated the temporal separation of successive targets and found that increasing temporal separation above 150ms for jumping-dot motion (Morgan & Turnbull,

1978) and above 300ms for slashed motion (Barnes & Asselman, 1992) decreases single-mode pursuit gain and increases saccade frequency, although some smooth pursuit is generated even at temporal separations as long as 1,000ms (Barnes & Asselman, 1992). To date, not much data is available on the effects of spatial separation on visual tracking eye movements, which is surprising given that spatial separation has been identified as an essential factor in the perception of apparent motion. At the level of receptive fields, the spatial limit d_{max} (Braddick, 1974) has been presumed to "represent the spatial range of the interactions that underlie directional selectivity within the receptive fields" (Sekuler et al., 1990, p. 210). Across receptive fields the apparent spatial separation is a critical parameter in perceiving apparent motion (Attneave & Block, 1973; Braddick, 1980). For these reasons, spatial separation would seem to be a very important parameter to examine when investigating visual tracking of apparent motion. At constant stimulus velocity the spatial separation between targets increases with increasing temporal separation, and it therefore follows logically that visual tracking performance would also decrease with increasing spatial separation, resulting in decreased single-mode pursuit gain and higher saccade frequency. Evidence from the smooth pursuit prediction literature also indicates that an increase in spatial separation would result in a decrease in eye velocity (Becker & Fuchs, 1985; Bennett & Barnes, 2003, 2004; Eckmiller & Mackeben, 1978; Madelain & Krauzlis, 2003; Von Noorden & Mackensen, 1962; Whittaker & Eaholtz, 1982). These studies mainly investigated the temporal disappearance of a moving target and therefore refer to effects of spatial separation on the already fully engaged smooth pursuit response. Nevertheless, the data from these studies suggest that increasing the spatial distance between target presentations would decrease smooth pursuit performance (see Chapter 2).

Furthermore, Heywood (1973) varied spatial separation from 0.25-1.00 deg using a sigma motion paradigm revealing more frequent saccades with increasing spatial separation for slower target speeds. Churchland and Lisberger (2000) systematically investigated the effects of both spatial and temporal target separation in monkeys, although focussing primarily on pursuit initiation rather than the maintained pursuit response. Their study tested various combinations of temporal and spatial separation at velocities ranging from 8.0-32.0 deg/s. Based on their findings, the authors proposed that smooth pursuit deficits during pursuit initiation and maintenance are caused by different mechanisms, because these deficits occurred at different combinations of the tested stimulus parameters. While pursuit initiation deficits in the tracking of apparent motion were explained in terms of visuo-motor motion processing problems, deficits during maintained pursuit were explained by a failure of the apparent motion stimulus to fully engage the pursuit system, because this in turn results in eye velocity memory deficits. Furthermore, at slow target velocities they found that pursuit initiation deficits were more likely to reflect the associated increase in temporal separation, while at faster velocities, they found that spatial separation was the limiting factor. Despite these worthwhile attempts to separate the effects of spatial and temporal target separation in apparent motion, it is generally very difficult to make clear inferences about spatial and temporal separation individually, as they cannot both be kept constant across changing target velocities. For example, a particular temporal separation is associated with large spatial separations at fast target speeds, and with small spatial separations at slow speeds, and vice versa. In conclusion, the effects of spatial separation on visual tracking eye movements have not yet been directly investigated using apparent motion with discrete step-displacement in humans.

With regard to the effects of target velocity on visual tracking eye movements, the data for visual tracking of apparent motion over wide a range of target velocities is sparse because many studies measure only one or two velocities and there is great variation in the choice of these target velocities. An exception is a study by Slaghuis, Hawkes, Holthouse, and Bruno (2007a), who examined a range of target speeds (5.0-35.0 deg/s) in a jumping-dot paradigm in order to investigate disordered tracking in schizophrenia compared with normal visual tracking. Their data suggest that differences between single-mode pursuit of continuous and apparent motion become increasingly larger with increasing target velocities (for observers with schizophrenia as well as controls), but their study did not directly compare tracking of continuous and apparent motion statistically.

The saccadic component of visual tracking of apparent motion has been largely ignored to date, and the few investigations of visual tracking of apparent motion stimuli focus on the smooth pursuit component of visual tracking. It is generally implied that the degraded apparent motion stimuli directly affect the smooth pursuit system, resulting in decreased single-mode pursuit eye velocity and gain (Barnes & Asselman, 1992; M. M. Churchland & Lisberger, 2000; Morgan & Turnbull, 1978). If any effects are reported relating to saccadic eye movements, they are generally viewed as a result of the smooth pursuit system failing, rather than being directly triggered by the apparent motion stimuli. In what may be too simplistic an explanation it is suggested that when smooth pursuit eye movements deteriorate, more frequent saccades are triggered by the position error caused by the eye lagging behind the target (see Chapter 4). In contrast, the findings of Experiment 1 have

demonstrated that the contribution of saccadic eye movements to visual tracking may be more complex and extensive, with independent variations of the frequency and characteristics of the generated saccades depending on stimulus velocity: the number of saccades generated to cross the motion trajectory of the target actually decreased as a function of target velocity, but the saccades were larger, faster and of longer duration at faster stimulus velocity. A similar pattern, but with a larger saccadic contribution, would also be expected for the tracking of apparent motion, but this has never been investigated.

In summary, the use of apparent motion stimuli in the motion perception literature and the few available studies on apparent motion induced visual tracking suggest that they have great potential to enhance our understanding of visual tracking. It is important to note that the jumping-dot and slashed motion paradigms have never been directly compared, and the effects of each type of apparent motion on the saccadic component of visual tracking have not yet been systematically investigated. In this context, the degrading of the motion signal into position and velocity information has the potential to tease out the differential effects of these signals on saccadic and pursuit eye movements. In addition, an investigation of the effects of stimulus duration and spatial separation may also reveal more about what conditions favour one or another eye movement during visual tracking. Because of the lack of research data in this area, the current study is rather exploratory in nature and examines a large range of spatial and temporal parameters across a wide range of stimulus velocities. The aim of Experiment 2 is to compare dual-mode visual tracking and individual saccadic and pursuit tracking components in response to jumping-dot and slashed

apparent motion stimuli with those of a continuously moving target for a wide range of spatio-temporal parameters.

Based on previous findings the following hypotheses are proposed:

1. Visual tracking of continuous motion is expected to be superior to tracking of both types of apparent motion, with poorer single-mode pursuit and a larger saccadic tracking contribution in response to both apparent motion paradigms (see Chapter 4).
2. Single-mode pursuit elicited by slashed motion is expected to be superior to single-mode pursuit of jumping-dot motion, due to the presence of the additional velocity signal in slashed motion, although based on Barnes and Asselman (1992), this effect is only expected for stimulus durations exceeding 30ms.
3. It is expected that increasing stimulus duration will decrease single-mode pursuit in response to jumping-dot motion (Barnes et al., 1987), but improve single-mode pursuit of slashed motion (Barnes & Asselman, 1992).
4. Differences in single-mode pursuit and saccadic eye movements in response to continuous and apparent motion stimuli are expected to be larger at faster target velocities (Slaghuis et al., 2007a).
5. Increasing spatial separation is expected to result in decreased single-mode pursuit and a larger saccadic contribution, consistent with what has been found for spatial separation in monkeys (M. M. Churchland & Lisberger, 2000) and for temporal separation in humans (Barnes & Asselman, 1992; Morgan & Turnbull, 1978).

Method

Participants

The three male and four female participants (age M=25.9, SD=6.7 years) in this study met the same inclusion criteria detailed in Experiment 1, and five of the participants in the present study also participated in Experiment 1. Written informed consent was obtained and the study had approval from the *Tasmanian Social Science Human Research Ethics Committee.*

Eye movement stimuli

A single black dot (0.25 deg) was generated as detailed in the *Method* section of Experiment 1. A continuously moving target and two different types of apparent motion stimuli were used. *Jumping-dot* apparent motion was generated using a succession of presentations of a stationary target stimulus and *slashed* apparent motion consisted of successive presentations of a moving target stimulus. The apparent motion stimuli were presented at three stimulus durations (20ms, 60ms, 100ms) and five spatial separations (0.5, 1.0, 2.0, 4.0, 5.0 deg) and all three motion stimuli were presented at nine constant stimulus velocities (2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s), with velocity for apparent motion calculated using the following formula: apparent velocity = spatial separation / [stimulus duration + temporal separation] (Castet, 1995; Kolers, 1972)

Procedure

Three full cycles of visual tracking (120.0 deg) were collected for each condition and data was collected in three separate sessions, each lasting approximately 60 minutes

including regular rest breaks. Participants were instructed to keep their eyes on the target at all times during recording, and head movements were minimised using a chin rest and bite board. The three types of motion stimuli, the three stimulus durations and the five spatial separations were presented to participants in alternating order to minimise order effects, but due to constraints of the visual tracking software stimulus velocities were presented in increasing order.

Eye movement recording

Eye movement recording was identical to that applied in Experiment 1.

Eye movement analysis

The same procedures reported in Experiment 1 were used to analyse the eye movements.

Measures

Single- and dual-mode eye velocity (deg/s) and gain (eye velocity / target velocity; eye velocity / apparent target velocity) were measured. To estimate the saccadic component of dual-mode tracking, frequency per second and per cycle were measured, as well as both time- and distance-based saccade ratio measures. Even though time-based measures were shown in Experiment 1 to be confounded by temporal variables they were analysed and reported in this study to evaluate these findings in response to apparent motion stimuli. Saccade amplitude (deg), duration (ms), and peak velocity (deg/s) were used to assess saccade characteristics, with corrections for pursuit velocity applied to amplitude and peak velocity (De Brouwer, Missal et al., 2002), as described in Experiment 1. Measures without the correction were also analysed, but the results for corrected and uncorrected measures were

highly similar, with smaller effect sizes for corrected measures, as was described in Experiment 1, and only the corrected, more stringent measures were reported.

Data analysis

Because Experiment 1 found no significant differences in the pattern of effects as a function of target velocity for right- and left-ward tracking, the data was collapsed across tracking direction for all analyses. Repeated measures ANOVAs with Greenhouse-Geisser corrections were used to analysed the effects of Type of Motion (Continuous, Slashed, Jumping-dot), Stimulus Duration (20ms, 60ms, 100ms), Spatial Separation (0.5, 1.0, 2.0, 4.0, 5.0 deg) and Target Velocity (2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s). Some combinations of spatial separation and stimulus durations did not generate all nine target velocities (particularly at 100ms stimulus duration), and for some analyses a set of repeated measures ANOVAs had to be conducted to cover all combinations, but strict Bonferroni adjustments to the alpha level were used for all multiple comparisons to maintain the familywise error rate at .05. Furthermore, a clerical error resulted in a number of missing values for the 7.5 deg/s target velocity for continuous motion stimuli, and analyses including the continuous motion paradigm were therefore only conducted for eight target velocities. Significant main effects were followed up using within-subjects contrasts (to check for linearity) or pairwise comparisons with Bonferroni-adjusted alpha levels, and significant interactions were examined using separate repeated measures ANOVAs and pairwise comparisons. Detailed statistical output files for all main analyses are provided in electronic format in Appendices E-J.

Results

The effects of stimulus duration

The apparent velocity range that could be generated depended on the combinations of spatial separation and stimulus durations, and particularly the longer stimulus durations did not cover the whole range of target speeds for all spatial separations. Four-factor ANOVAs were therefore conducted initially in order to compare spatial and temporal parameters of the two apparent motion paradigms across all target velocities. Five 2 [Apparent Motion: Jumping-dot, Slashed Motion] X 3 [Stimulus Duration: 20, 60, 100ms] X 1-5 [Spatial Separation: 0.5, 1.0, 2.0, 4.0, 5.0 deg] X 1-9 [Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s] repeated measures ANOVAs (using Greenhouse-Geisser corrections) were conducted for each dependent variable. Even though this large set of ANOVAs included some overlap, and therefore some redundancy of results, it ensured that the whole range of spatial separations and target speeds could be compared across the three stimulus durations. Bonferroni adjustments to the alpha level (α=.01) were strictly used to ensure that the familywise error rate was maintained at .05 (detailed output files for these analyses are presented in Appendices E and F). These sets of ANOVAs produced a high volume of results, and for the sake of clarity the results of these analyses are reported in separate sections, depending on what factors they relate to. All results for Stimulus Duration are summarised in Table 3 and reported in the current section, but the results from these analyses pertaining to the comparison of the two apparent motion paradigms are reported in Table 8 (p.193), in the section that focuses on the comparison between jumping-dot and slashed motion stimuli.

Table 3. Summary of main effects and interactions for Stimulus Duration

Measure	Spatial Separation	Target Velocity	Main effect of Stimulus Duration	Apparent Motion X Stimulus Duration
Dual-Mode Tracking	**(deg)**	**(deg/s)**		
Dual-Mode Eye Velocity	0.5,1,2,4,5	2.5	$F(2,10)=0.3,\eta^2=.06$	$F(2,8)=2.0,\eta^2=.29$
	1,2,4,5	2.5,5,7.5	$F(2,10)=0.6,\eta^2=.12$	$F(2,10)=1.4,\eta^2=.21$
	2,4,5	2.5,5,7.5,10,15	$F(1,6)=0.6,\eta^2=.11$	$F(2,8)=1.3,\eta^2=.21$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,6)=0.8,\eta^2=.15$	$F(1,7)=1.0,\eta^2=.17$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,6)=1.5,\eta^2=.23$	$F(1,6)=1.8,\eta^2=.27$
Dual-Mode Gain	0.5,1,2,4,5	2.5	$F(2,10)=0.3,\eta^2=.05$	$F(2,8)=2.0,\eta^2=.29$
	1,2,4,5	2.5,5,7.5	$F(2,9)=0.4,\eta^2=.07$	$F(2,10)=1.7,\eta^2=.25$
	2,4,5	2.5,5,7.5,10,15	$F(1,7)=0.5,\eta^2=.09$	$F(2,9)=1.4,\eta^2=.22$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=1.2,\eta^2=.19$	$F(2,8)=1.4,\eta^2=.21$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=1.9,\eta^2=.28$	$F(1,7)=2.0,\eta^2=.28$
Single-Mode Pursuit				
Single-Mode Eye Velocity	0.5,1,2,4,5	2.5	$F(2,9)=1.3,\eta^2=.21$	**$F(2,9)=14.7,\eta^2=.75$***
	1,2,4,5	2.5,5,7.5	$F(2,8)=4.5,\eta^2=.47$	**$F(1,7)=16.3,\eta^2=.77$***
	2,4,5	2.5,5,7.5,10,15	$F(2,10)=3.1,\eta^2=.38$	**$F(1,7)=12.3,\eta^2=.71$***
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,10)=1.7,\eta^2=.26$	$F(1,7)=5.3,\eta^2=.52$^
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,9)=5.3,\eta^2=.52$^	$F(1,6)=6.6,\eta^2=.57$^
Single-Mode Gain	0.5,1,2,4,5	2.5	$F(2,9)=1.3,\eta^2=.21$	**$F(2,9)=14.9,\eta^2=.75$***
	1,2,4,5	2.5,5,7.5	$F(1,7)=3.7,\eta^2=.43$	**$F(1,7)=18.0,\eta^2=.78$***
	2,4,5	2.5,5,7.5,10,15	$F(2,9)=3.4,\eta^2=.40$	**$F(1,7)=14.5,\eta^2=.74$***
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,10)=2.8,\eta^2=.36$	**$F(1,7)=9.3,\eta^2=.65$***
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,9)=4.7,\eta^2=.49$^	$F(1,6)=9.4,\eta^2=.65$^
Saccades				
Saccade Frequency per second	0.5,1,2,4,5	2.5	$F(1,6)=0.5,\eta^2=.10$	$F(2,8)=0.3,\eta^2=.05$
	1,2,4,5	2.5,5,7.5	$F(1,6)=1.6,\eta^2=.25$	$F(2,9)=0.6,\eta^2=.11$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=3.4,\eta^2=.41$	$F(2,8)=1.2,\eta^2=.20$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,8)=2.0,\eta^2=.28$	$F(2,10)=0.6,\eta^2=.11$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,8)=5.6,\eta^2=.53$^	$F(2,9)=0.4,\eta^2=.08$
Saccade Frequency per cycle	0.5,1,2,4,5	2.5	$F(1,6)=0.5,\eta^2=.10$	$F(2,8)=0.3,\eta^2=.05$
	1,2,4,5	2.5,5,7.5	$F(1,6)=1.3,\eta^2=.21$	$F(2,9)=0.6,\eta^2=.11$
	2,4,5	2.5,5,7.5,10,15	$F(1,6)=2.5,\eta^2=.33$	$F(2,9)=1.1,\eta^2=.18$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,7)=2.4,\eta^2=.33$	$F(2,9)=0.4,\eta^2=.07$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,7)=3.6,\eta^2=.42$	$F(2,9)=0.1,\eta^2=.01$
Saccade Amplitude	0.5,1,2,4,5	2.5	$F(1,7)=1.7,\eta^2=.25$	$F(1,7)=5.4,\eta^2=.52$^
	1,2,4,5	2.5,5,7.5	$F(2,8)=1.3,\eta^2=.20$	$F(1,7)=9.0,\eta^2=.64$^
	2,4,5	2.5,5,7.5,10,15	$F(2.8)=1.5,\eta^2=.23$	$F(1,6)=8.4,\eta^2=.63$^
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,10)=0.4,\eta^2=.07$	$F(1,6)=2.6,\eta^2=.35$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,11)=0.2,\eta^2=.03$	$F(2,11)=1.3,\eta^2=.18$
Saccade Duration	0.5,1,2,4,5	2.5	$F(2,10)=0.2,\eta^2=.04$	$F(2,8)=3.8,\eta^2=.43$
	1,2,4,5	2.5,5,7.5	$F(2,9)=0.5,\eta^2=.09$	$F(2,8)=5.5,\eta^2=.53$^
	2,4,5	2.5,5,7.5,10,15	$F(2,8)=0.9,\eta^2=.15$	$F(2,9)=5.1,\eta^2=.51$^
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,9)=0.5,\eta^2=.09$	$F(2,8)=1.9,\eta^2=.27$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,10)=0.5,\eta^2=.08$	$F(2,10)=0.4,\eta^2=.08$
Saccade Peak Velocity	0.5,1,2,4,5	2.5	$F(2,9)=2.4,\eta^2=.32$	$F(2,8)=3.0,\eta^2=.38$
	1,2,4,5	2.5,5,7.5	$F(2,9)=0.3,\eta^2=.05$	$F(1,7)=5.8,\eta^2=.54$^
	2,4,5	2.5,5,7.5,10,15	$F(2,10)=0.3,\eta^2=.06$	$F(1,7)=7.3,\eta^2=.60$^
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,9)=0.2,\eta^2=.04$	$F(1,6)=3.1,\eta^2=.38$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(2,9)=0.1,\eta^2=.00$	$F(1,5)=2.2,\eta^2=.30$
Time-based Saccade Ratio	0.5,1,2,4,5	2.5	$F(1,5)=0.3,\eta^2=.06$	$F(1,6)=0.5,\eta^2=.09$
	1,2,4,5	2.5,5,7.5	$F(1,5)=0.8,\eta^2=.13$	$F(2,8)=0.8,\eta^2=.15$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=1.6,\eta^2=.24$	$F(1,7)=1.6,\eta^2=.25$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(2,9)=1.5,\eta^2=.23$	$F(2,10)=1.7,\eta^2=.25$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,7)=2.7,\eta^2=.35$	$F(2,9)=1.2,\eta^2=.19$
Distance-based Saccade Ratio	0.5,1,2,4,5	2.5	$F(2,8)=1.6,\eta^2=.24$	$F(1,6)=8.3,\eta^2=.63$^
	1,2,4,5	2.5,5,7.5	$F(2,9)=1.6,\eta^2=.24$	$F(1,5)=10.3,\eta^2=.67$^
	2,4,5	2.5,5,7.5,10,15	$F(2,8)=0.3,\eta^2=.06$	$F(2,8)=7.4,\eta^2=.60$^
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,6)=0.2,\eta^2=.03$	$F(2,8)=6.0,\eta^2=.55$^
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,7)=0.5,\eta^2=.09$	$F(2,8)=3.1,\eta^2=.38$

Note: For each dependent variable a set of five ANOVAs were conducted, together covering the whole range of stimulus durations, spatial separations and target velocities. There were no other significant effects involving Stimulus Duration and no significant 3-or-4-way interactions. ^$.05>p>.01$, *$p<.01$; significant effects are in bold.

There were no significant main effects of stimulus duration on any of the dependent variables (see Table 3) and the only significant findings with regard to stimulus duration were a significant interaction between stimulus duration and the type of apparent motion for single-mode pursuit eye velocity and single-mode pursuit gain, which will be described and discussed in the section reporting the direct comparison of the two apparent motion stimuli (Table 8, p.193). Because there were no other significant effects involving stimulus duration, this factor was not included in further analyses that did not involve a direct comparison of jumping-dot and slashed motion, and all other analyses were conducted at 20ms stimulus duration only, because this duration allowed for the largest velocity range. The two apparent motion paradigms are first analysed and presented individually, allowing a more thorough and direct examination of each type of apparent motion; how visual tracking compared to that of continuous motion, as well as the effects of spatial separation and target velocity. Then visual tracking of jumping-dot and slashed motion stimuli are directly compared, in order to investigate similarities and differences between the two types of apparent motion.

A comparison of visual tracking of continuous and jumping-dot motion stimuli

In order to compare visual tracking of jumping-dot stimuli with continuous motion, 2 [Type of Motion: Continuous, Jumping-dot] X 8 [Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s] repeated measures ANOVAs were conducted for all dependent variables, separately for each of the five spatial separations (with only six velocities [2.5-25.0 deg/s] for 0.5 deg spatial separation). Greenhouse-Geisser corrections and a Bonferroni-adjusted alpha level of .01 were used. The findings are summarised in Table 4 and statistical output files are provided in electronic Appendix G).

Table 4. Summary of main effects and interactions comparing visual tracking of continuous and jumping-dot motion across target velocity for each spatial separation

Measure	Spatial Separation	Main Effect Type of Motion	Main Effect of Velocity	Type of Motion X Velocity Interaction
Dual-Mode Tracking	(deg)			
Dual-Mode Eye Velocity	0.5	$F(1,6)=0.8,\eta^2=.12$	**$F(1,8)=312.1,\eta^2=.98$****	$F(1,8)=1.8,\eta^2=.23$
	1.0	$F(1,6)=0.1,\eta^2=.01$	**$F(1,7)=50.1,\eta^2=.89$****	$F(2,9)=1.4,\eta^2=.19$
	2.0	$F(1,6)=1.9,\eta^2=.25$	**$F(2,10)=103.6,\eta^2=.95$****	$F(2,12)=3.4,\eta^2=.36$
	4.0	$F(1,6)=0.0,\eta^2=.00$	**$F(1,7)=53.7,\eta^2=.90$****	$F(2,13)=4.1,\eta^2=.41$
	5.0	$F(1,6)=0.9,\eta^2=.13$	**$F(1,9)=53.5,\eta^2=.90$****	$F(2,14)=1.6,\eta^2=.21$
Dual-Mode Gain	0.5	$F(1,6)=2.9,\eta^2=.33$	$F(2,12)=5.6,\eta^2=.48$^	$F(2,15)=1.0,\eta^2=.14$
	1.0	$F(1,6)=3.7,\eta^2=.38$	$F(1,7)=5.0,\eta^2=.45$	$F(3,16)=0.9,\eta^2=.13$
	2.0	$F(1,6)=9.5,\eta^2=.61$^	$F(2,11)=5.8,\eta^2=.49$^	$F(2,13)=1.5,\eta^2=.20$
	4.0	$F(1,6)=1.3,\eta^2=.18$	$F(1,9)=3.0,\eta^2=.33$	$F(3,18)=4.3,\eta^2=.42$^
	5.0	$F(1,6)=0.0,\eta^2=.00$	$F(2,14)=4.5,\eta^2=.43$^	$F(3,20)=1.3,\eta^2=.18$
Single-mode Pursuit				
Single-Mode Eye Velocity	0.5	$F(1,6)=11.5,\eta^2=.66$ ^	**$F(1,8)=103.5,\eta^2=.95$****	**$F(2,9)=12.5,\eta^2=.68$***
	1.0	$F(1,6)=5.1,\eta^2=.46$	**$F(1,8)=30.2,\eta^2=.83$****	$F(2,12)=2.1,\eta^2=.26$
	2.0	**$F(1,6)=21.9,\eta^2=.79$***	**$F(1,7)=22.4,\eta^2=.79$***	$F(2,8)=2.4,\eta^2=.28$
	4.0	**$F(1,6)=50.7,\eta^2=.89$****	**$F(1,7)=23.0,\eta^2=.79$***	**$F(2,14)=6.1,\eta^2=.51$***
	5.0	**$F(1,6)=58.8,\eta^2=.91$ ****	**$F(1,8)=23.1,\eta^2=.79$***	**$F(2,12)=10.7,\eta^2=.64$***
Single-Mode Gain	0.5	$F(1,6)=1.2,\eta^2=.16$	$F(2,11)=6.3,\eta^2=.51$^	$F(2,13)=5.0,\eta^2=.45$^
	1.0	$F(1,6)=2.7,\eta^2=.31$	$F(2,11)=3.5,\eta^2=.37$	**$F(2,14)=5.8,\eta^2=.49$***
	2.0	**$F(1,6)=15.9,\eta^2=.73$***	$F(2,10)=5.6,\eta^2=.48$^	**$F(2,13)=8.9,\eta^2=.60$***
	4.0	**$F(1,6)=59.3,\eta^2=.91$****	$F(1,9)=2.2,\eta^2=.27$	**$F(2,12)=9.1,\eta^2=.60$***
	5.0	**$F(1,6)=75.7,\eta^2=.93$****	$F(1,9)=1.3,\eta^2=.18$	$F(2,13)=5.2,\eta^2=.46$^
Saccades				
Saccade Frequency per second	0.5	$F(1,5)=2.9,\eta^2=.37$	**$F(2,8)=15.9,\eta^2=.76$***	$F(2,10)=4.4,\eta^2=.47$^
	1.0	$F(1,5)=1.6,\eta^2=.25$	**$F(2,9)=18.4,\eta^2=.79$***	**$F(3,14)=8.3,\eta^2=.62$***
	2.0	**$F(1,5)=70.0,\eta^2=.93$****	**$F(2,12)=17.2,\eta^2=.76$****	$F(2,10)=3.4,\eta^2=.40$
	4.0	**$F(1,5)=29.6,\eta^2=.86$***	**$F(2,12)=21.6,\eta^2=.81$****	$F(2,12)=1.7,\eta^2=.26$
	5.0	**$F(1,5)=48.5,\eta^2=.91$***	**$F(2,11)=32.2,\eta^2=.87$****	$F(3,13)=1.0,\eta^2=.17$
Saccade Frequency per cycle	0.5	$F(1,6)=5.9,\eta^2=.50$	**$F(1,7)=11.4,\eta^2=.66$***	**$F(2,11)=21.5,\eta^2=.78$****
	1.0	$F(1,6)=5.3,\eta^2=.47$	**$F(2,10)=25.5,\eta^2=.81$****	**$F(2,8)=19.3,\eta^2=.76$***
	2.0	**$F(1,6)=22.1,\eta^2=.79$***	**$F(1,8)=24.3,\eta^2=.80$***	**$F(2,12)=45.3,\eta^2=.88$****
	4.0	$F(1,6)=9.2,\eta^2=.60$^	**$F(2,11)=58.6,\eta^2=.91$****	**$F(1,8)=17.0,\eta^2=.74$***
	5.0	$F(1,6)=9.0,\eta^2=.60$^	**$F(2,11)=53.0,\eta^2=.90$****	**$F(2,10)=13.8,\eta^2=.70$***
Saccade Amplitude	0.5	$F(1,6)=4.8,\eta^2=.45$	$F(1,7)=8.8,\eta^2=.60$^	$F(2,10)=0.9,\eta^2=.13$
	1.0	$F(1,6)=2.3,\eta^2=.28$	**$F(1,8)=10.4,\eta^2=.63$***	$F(1,7)=0.4,\eta^2=.07$
	2.0	$F(1,6)=7.9,\eta^2=.57$^	**$F(1,9)=10.1,\eta^2=.63$***	$F(1,9)=1.1,\eta^2=.16$
	4.0	$F(1,6)=10.5,\eta^2=.64$^	**$F(2,10)=14.2,\eta^2=.70$***	$F(1,8)=0.3,\eta^2=.05$
	5.0	**$F(1,6)=24.4,\eta^2=.80$***	$F(1,8)=6.2,\eta^2=.51$ ^	$F(2,15)=2.3,\eta^2=.27$
Saccade Duration	0.5	$F(1,6)=1.8,\eta^2=.23$	**$F(1,8)=31.5,\eta^2=.84$****	$F(1,8)=0.2,\eta^2=.03$
	1.0	$F(1,6)=1.4,\eta^2=.19$	**$F(2,14)=17.1,\eta^2=.74$****	$F(3,15)=1.1,\eta^2=.16$
	2.0	$F(1,6)=1.7,\eta^2=.22$	**$F(3,19)=32.9,\eta^2=.84$****	$F(2,15)=1.6,\eta^2=.22$
	4.0	$F(1,6)=8.0,\eta^2=.57$^	**$F(3,19)=20.0,\eta^2=.77$****	$F(3,17)=3.8,\eta^2=.39$^
	5.0	$F(1,6)=9.9,\eta^2=.62$^	**$F(3,19)=24.0,\eta^2=.80$****	$F(2,12)=2.0,\eta^2=.25$
Saccade Peak Velocity	0.5	$F(1,6)=1.6,\eta^2=.21$	**$F(2,11)=20.2,\eta^2=.77$****	$F(2,13)=0.1,\eta^2=.02$
	1.0	$F(1,6)=3.7,\eta^2=.38$	**$F(3,17)=10.9,\eta^2=.65$****	$F(1,9)=0.3,\eta^2=.05$
	2.0	$F(1,6)=5.7,\eta^2=.49$	**$F(2,12)=9.3,\eta^2=.61$***	$F(2,10)=0.6,\eta^2=.09$
	4.0	$F(1,6)=4.9,\eta^2=.45$	**$F(3,16)=15.3,\eta^2=.72$****	$F(2,9)=0.4,\eta^2=.06$
	5.0	$F(1,6)=5.3,\eta^2=.47$	**$F(2,12)=8.7,\eta^2=.59$***	$F(3,19)=0.5,\eta^2=.07$
Time-based Saccade Ratio	0.5	$F(1,6)=0.0,\eta^2=.00$	**$F(2,11)=31.1,\eta^2=.84$****	$F(1,8)=5.0,\eta^2=.45$^
	1.0	$F(1,6)=0.0,\eta^2=.00$	**$F(1,8)=22.2,\eta^2=.79$***	$F(2,11)=1.9,\eta^2=.24$
	2.0	$F(1,6)=5.5,\eta^2=.48$	**$F(1,9)=30.9,\eta^2=.84$****	$F(2,12)=0.4,\eta^2=.07$
	4.0	$F(1,6)=9.4,\eta^2=.61$	**$F(2,9)=31.7,\eta^2=.84$****	$F(2,12)=0.2,\eta^2=.04$
	5.0	$F(1,6)=11.1,\eta^2=.65$^	**$F(2,11)=54.3,\eta^2=.90$****	$F(1,7)=0.8,\eta^2=.11$
Distance-based Saccade Ratio	0.5	$F(1,6)=3.4,\eta^2=.36$	$F(1,7)=2.2,\eta^2=.27$	**$F(2,15)=5.8,\eta^2=.49$***
	1.0	$F(1,6)=6.0,\eta^2=.50$^	$F(2,10)=5.8,\eta^2=.49$^	$F(2,11)=2.1,\eta^2=.26$
	2.0	$F(1,6)=5.0,\eta^2=.46$	$F(1,6)=2.6,\eta^2=.30$	$F(1,6)=1.3,\eta^2=.18$
	4.0	$F(1,6)=12.3,\eta^2=.67$^	$F(2,14)=2.2,\eta^2=.27$	$F(3,16)=1.4,\eta^2=.19$
	5.0	$F(1,6)=9.4,\eta^2=.61$^	$F(1,7)=2.1,\eta^2=.26$	$F(1,7)=1.4,\eta^2=.19$

Note: ^.05>p>.01, *p<.01, **p<.001; significant effects are in bold.

Dual-mode tracking of continuous and jumping-dot motion stimuli

There were no significant differences in dual-mode tracking eye velocity or gain at any of the spatial separations between continuous and jumping-dot motion stimuli (see Table 4, Figure 14). This shows that when saccadic and smooth pursuit eye movements are combined even a highly degraded apparent motion stimulus can be tracked as well as a continuously moving target. As expected, dual-mode eye velocity increased significantly with increasing target velocity for both types of motion stimuli, with the eyes keeping up with the target stimulus. Dual-mode gain was not affected by target velocity for either continuous or jumping-dot apparent motion, which demonstrates that the performance of dual-mode tracking, combining saccadic and pursuit eye movements, is very accurate up to speeds of 35.0 deg/s.

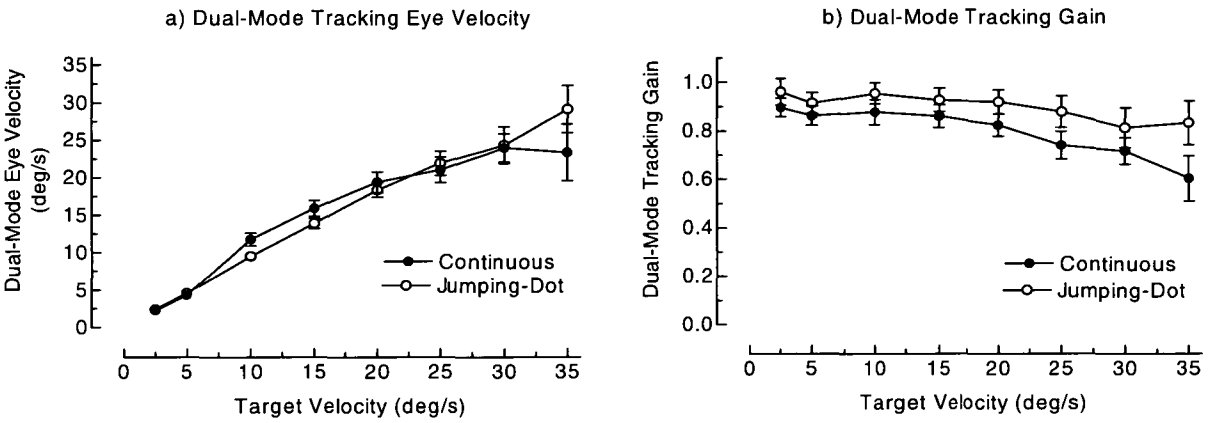

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Figure 14. (a) Eye velocity and (b) gain for dual-mode tracking in response to continuous and jumping-dot motion averaged for spatial separation. Error bars depict standard error of the mean (*SE*).

Single-mode pursuit of jumping-dot motion stimuli

As was expected, single-mode pursuit eye velocity increased significantly with increasing target velocity (see Table 4), and single-mode pursuit eye velocity was significantly faster in response to continuous than jumping-dot stimuli, but only when

spatial separation was 2.0 deg or more. The interaction between the type of motion and target velocity was significant for 0.5, 4.0, and 5.0 deg spatial separations. As illustrated in Figure 15, pairwise comparisons showed that at 0.5 deg spatial separation task differences were only significant for 20.0 deg/s target velocity, with greater single-mode pursuit eye velocity in response to continuous than jumping-dot stimuli. At 1.0 deg spatial separation there were no significant differences in eye velocity for continuous and jumping-dot stimuli. When spatial separations were 2.0, 4.0 and 5.0 deg single-mode eye velocity was significantly faster in response to continuous than jumping-dot motion stimuli for virtually all target speeds, and these differences increased significantly as a function of target velocity.

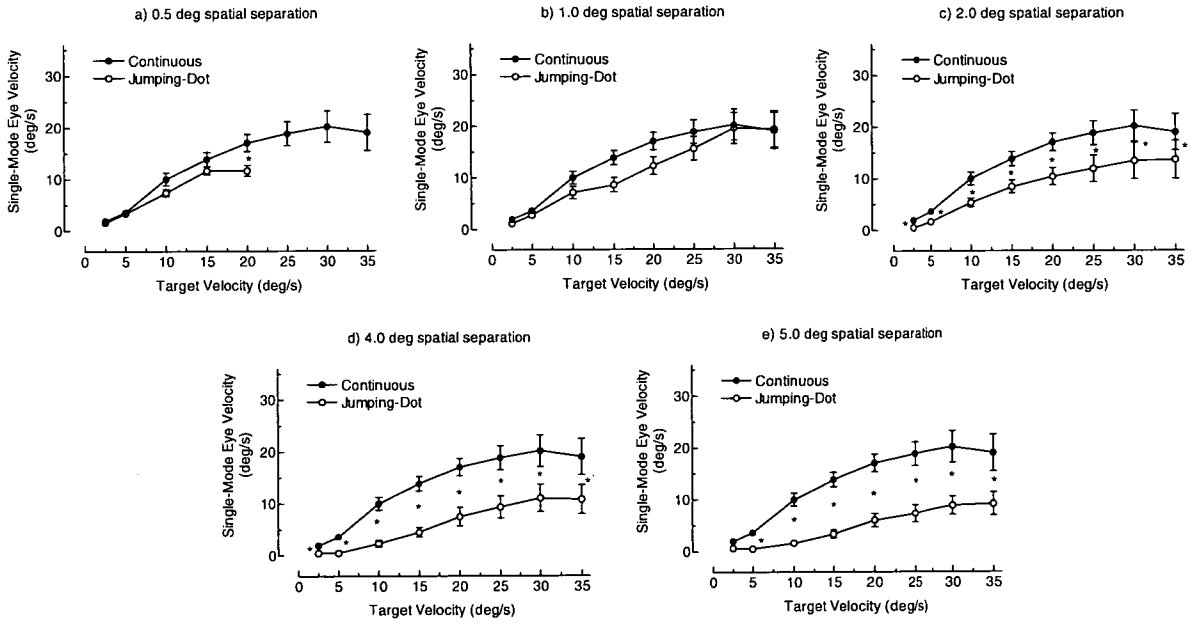

Figure 15. The interaction between the type of motion and target velocity was significant for 0.5, 4.0 and 5.0 degree spatial separation on single-mode pursuit eye velocity (* denote significant differences, $p<0.006$; error bars depict *SE*). Single-mode eye velocity for continuous motion followed a significant linear trend [$F(1,6)=28.0, p<.01, \eta^2=.82$]; jumping-dot motion also increased linearly for all spatial separations: (a) 0.5 deg: [$F(1,6)=150.3, p<.001, \eta^2=.96$], (b) 1.0 deg: [$F(1,6)=31.6, p<.01, \eta^2=.84$], (c) 2.0 deg: [$F(1,6)=13.6, p=0.1, \eta^2=.69$], (d) 4.0 deg: [$F(1,6)=15.0, p<.01, \eta^2=.71$] and (e) 5.0 deg: [$F(1,6)=17.9, p<.01, \eta^2=.75$].

Single-mode pursuit gain for jumping-dot motion was also significantly lower than for continuous motion when spatial separation was 2.0 deg or more (see Table 4). There was a significant interaction between the type of motion and target velocity when spatial separation was 1.0, 2.0, and 4.0 deg, and the interaction approached significance ($.05>p>.01$) for spatial separations of 0.5 and 5.0 deg. As illustrated in Figure 16, the functions for smooth pursuit eye movements elicited by continuous and jumping-dot motion stimuli were strikingly different as a function of target velocity. For continuous motion, single-mode pursuit gain decreased linearly when target velocity increased. In contrast, single-mode pursuit gain elicited by jumping-dot motion followed a quadratic trend and low pursuit gain was associated with both slow and fast target velocities. It is important to note that differences in single-mode pursuit gain of continuous and jumping-dot motion stimuli were most pronounced at slow target velocities (as shown by Bonferroni-adjusted pairwise comparisons, see Figure 16) and single-mode pursuit gain was similar for the two types of motion at moderate to fast velocities (depending on spatial separation).

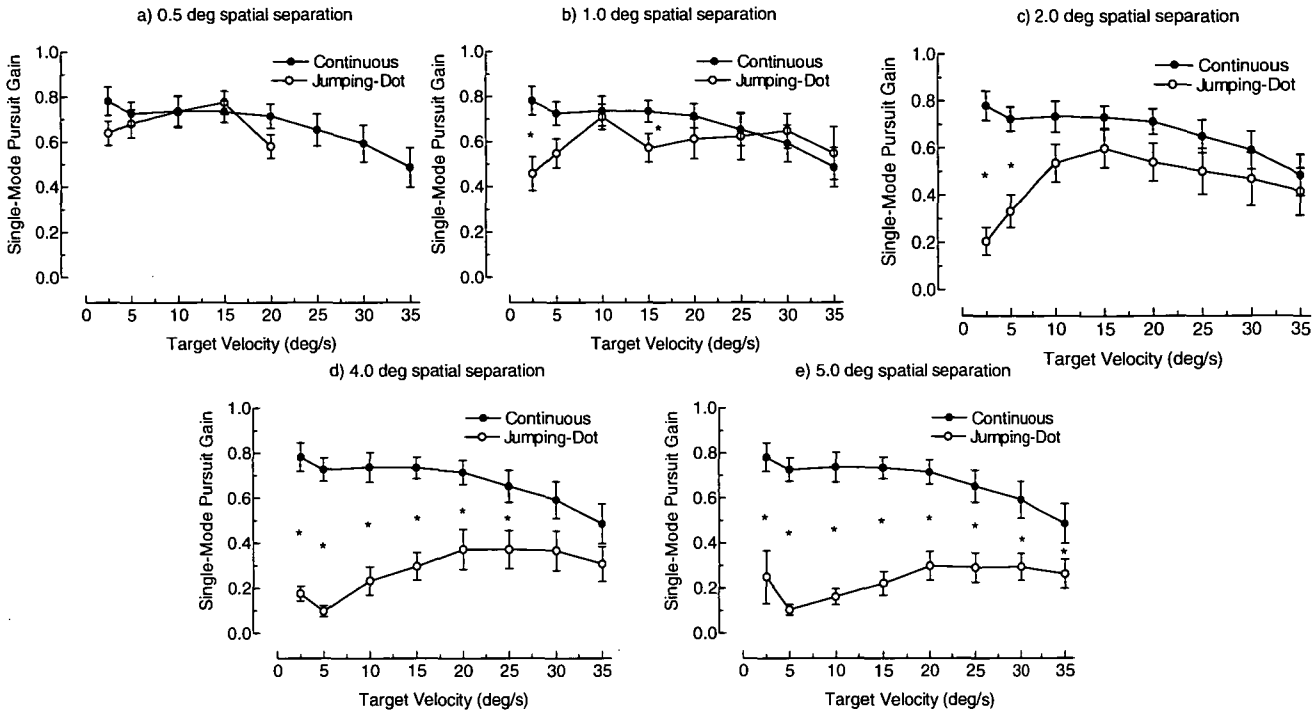

Figure 16. The interaction between the type of motion and target velocity for each spatial separations on single-mode pursuit gain (* denote significant differences, $p<.006$; error bars depict *SE*). Single-mode pursuit gain to continuous motion decreased linearly [$F(1,6)=9.3, p<.05, \eta^2=.55$]; single-mode pursuit gain for jumping-dot apparent motion followed a quadratic trend at (a) 0.5 deg: $F(1,6)=23.0, p<.01, \eta^2=.79$ (b) 1.0 deg: $F(1,6)=14.6, p<.01, \eta^2=.71$ (c) 2.0 deg: $F(1,6)=42.4, p<.01, \eta^2=.88$ (d) 4.0 deg: $F(1,6)=11.1, p<.05, \eta^2=.65$, and a cubic trend at (e) 5.0 deg: $F(1,6)=7.8, p<.05, \eta^2=.56$.

An examination of the quadratic function of single-mode pursuit gain for jumping-dot motion as a function of target velocity (Figure 16) reveals that the peak for single-mode pursuit gain occurs at different target velocities for different spatial separations. When spatial separation was 0.5-2.0 deg single-mode pursuit gain peaked at target velocities 10.0-15.0 deg/s, while optimal pursuit gain at 4.0 and 5.0 deg spatial separation was at 20.0-30.0 deg/s target speed, and at spatial separation of 1.0 deg, two peaks were evident at both 10.0 and 30.0 deg/s. These results indicate that peak single-mode pursuit gain in response to jumping-dot motion shifts to faster target velocities when spatial separation is increased.

Main sequence relationship of saccades elicited by jumping-dot motion stimuli

The main sequence relationships for jumping-dot motion for all participants are displayed in Figure 17. The saccades generated in the tracking of jumping-dot apparent motion follow the general linear main sequence relationship found in response to stationary and continuously moving targets (De Brouwer, Missal et al., 2002; Experiment 1). This demonstrates that saccades produced in the tracking of apparent motion have the same general dynamics, and presumably the same underlying mechanisms, as saccades in response to continuous motion and stationary targets.

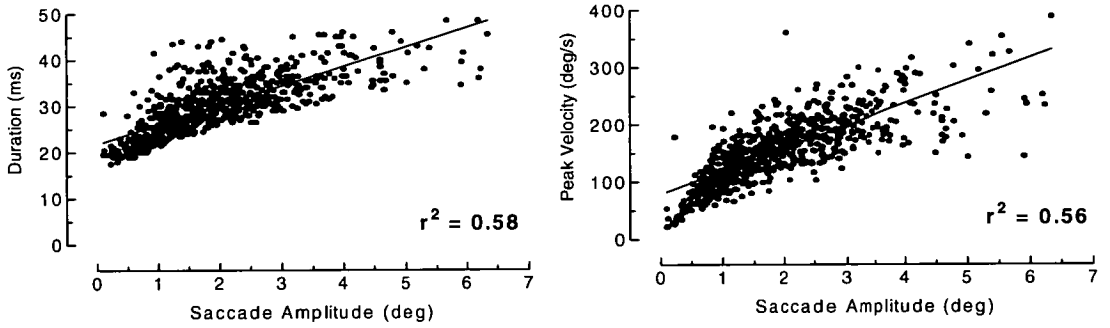

Figure 17. Main sequence relationship between mean saccade amplitude and mean saccade duration and peak velocity for each participant for saccades generated in the tracking of all combinations of spatial separation and target velocity for jumping-dot motion stimuli.

Frequency of saccades elicited by jumping-dot motion stimuli

As summarised in Table 4 and illustrated in Figures 18 and 19, saccade frequency per second and per cycle had quite different patterns as a function of target velocity, similar to what was found in response to continuous motion in Experiment 1. The number of saccades per second increased significantly with increasing target velocity in response to both continuous and jumping-dot motion stimuli. Also, for spatial

separations of 2.0 deg or more, there were a greater number of saccades per second when tracking jumping-dot motion than continuous motion.

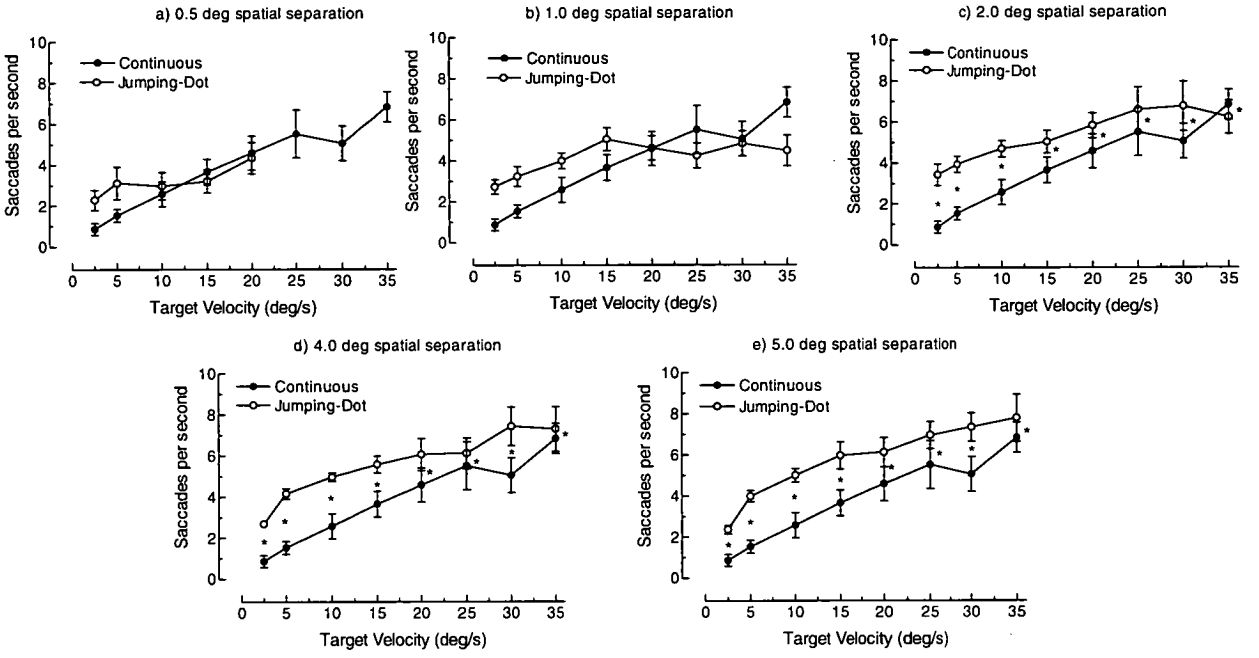

Figure 18. Saccade frequency per second for continuous and jumping-dot motion stimuli as a function of target velocity for each spatial separation (* denote significant differences, $p<.006$; error bars depict *SE*).

The number of saccades per cycle (per 40.0 deg of visual tracking) decreased with increasing target velocity and the interaction between type of motion and velocity was significant for all spatial separations (Table 4). Figure 19 illustrates that there were more saccades per cycle in the tracking of jumping-dot than continuous motion, but only for slow target velocities (2.5-5.0 deg/s). With increasing spatial separation, this difference in saccade frequency extended to faster target velocities.

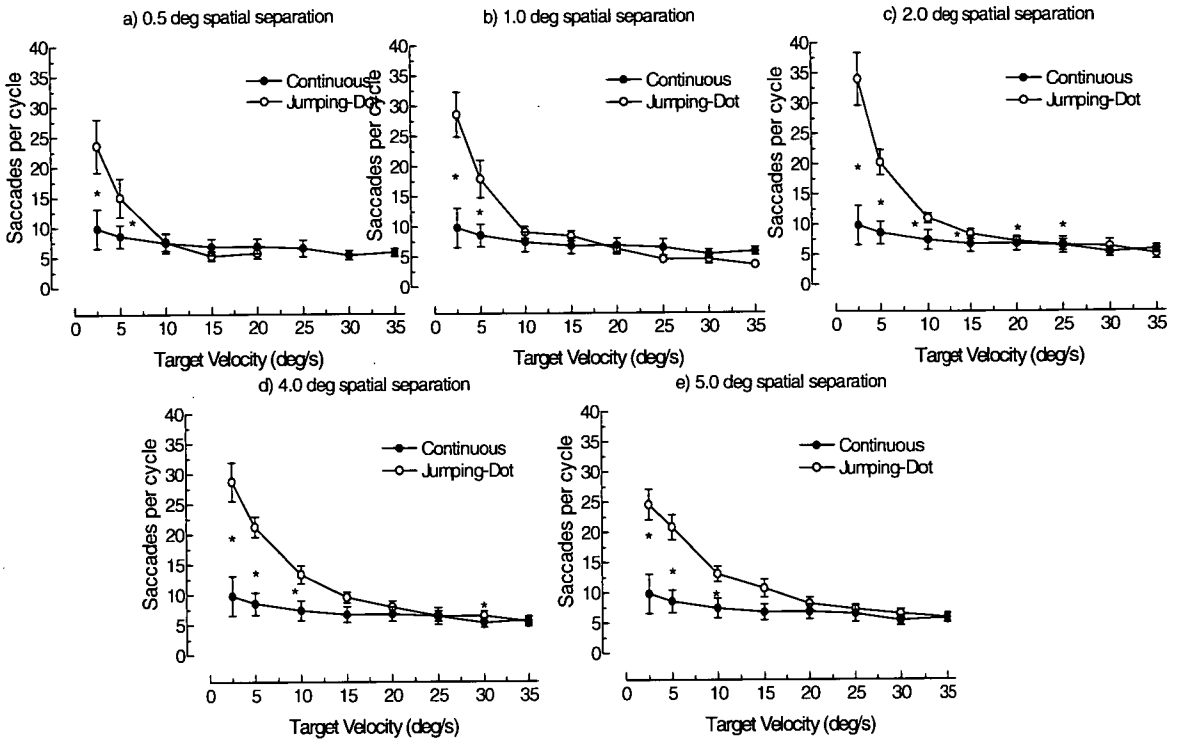

Figure 19. Saccade frequency per cycle for continuous and jumping-dot motion as a function of target velocity for each spatial separation (* denote significant differences, $p<.006$; error bars depict *SE*).

Characteristics of saccades elicited by jumping-dot motion stimuli

For both types of motion stimuli, saccades became increasingly larger, faster and of longer duration with increasing target velocity (see Table 4), as illustrated in Figure 20. There were no significant differences in the characteristics of saccades generated in the tracking of continuous and jumping-dot motion stimuli, except a tendency for saccade amplitude to be larger in response to jumping-dot stimuli than for continuous motion, but this reached significant levels only when the spatial separation was 5.0 deg.

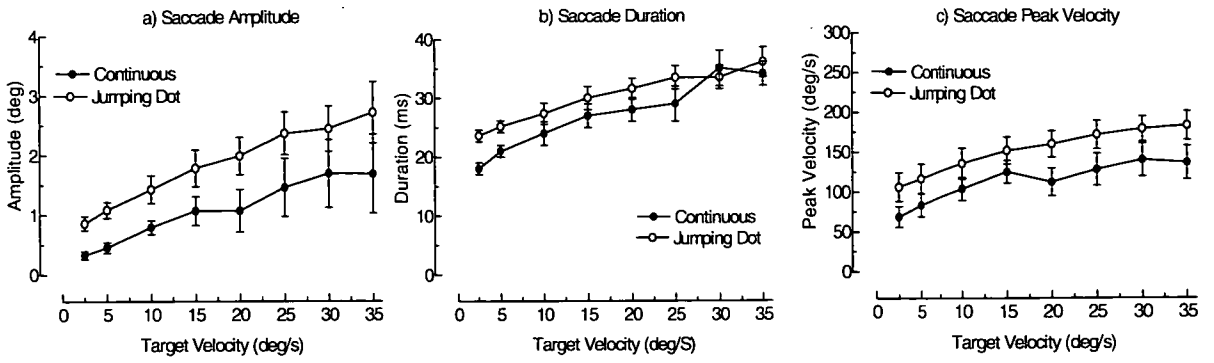

Figure 20. Saccade characteristics in response to continuous and jumping-dot motion stimuli for (a) saccade amplitude (b) duration and (c) peak velocity as a function of target velocity (averaged for spatial separation, error bars depict *SE*).

Ratio of saccadic versus smooth pursuit eye movements in the visual tracking of jumping-dot motion stimuli

There was no difference in the tracking of continuous and jumping-dot motion stimuli with regard to both time-based and distance-based ratios of saccadic versus smooth pursuit eye movements. As illustrated in Table 4 and Figure 21, there was a tendency for the distance-based ratio of saccadic eye movements elicited by jumping-dot stimuli to be larger than for continuous motion, but this did not reach the stringent 0.01 significance level due to the large variability in the data (as indicated by the large *SEs* in Figure 21). The duration of time spent in saccadic eye movements when tracking jumping-dot apparent motion increased significantly and linearly with increasing target velocity for both continuous and jumping-dot motion. This is consistent with the findings presented in Figure 18, whereby for both types of motion more saccades were generated per second with increasing target velocity. However, as outlined in Chapter 6, time-based measures are affected by differences in the dynamics of saccadic and smooth pursuit eye movements, as well as the overall tracking time, and are therefore not accurate measures of the saccadic contribution.

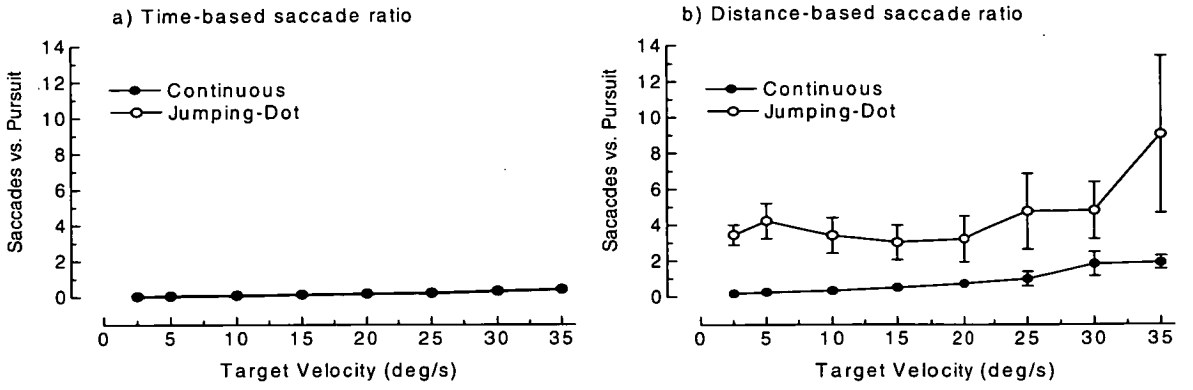

Figure 21. (a) Time-based and (b) distance-based ratio of saccadic saccadic versus pursuit eye movements in the tracking of continuous and jumping-dot motion (averaged for spatial separation, error bars depcit *SE*).

There was no significant effect of stimulus velocity on the distance-based saccadic ratio for jumping-dot stimuli, which indicates that the ratio of the distance covered by saccadic versus pursuit eye movements did not change significantly with increasing target speed (see Table 4), although the quadratic trend did approach significance [$F(1,6)=5.2, p=.06, \eta^2=.46$]. This shows that although the absolute number of saccades per spatial distance changed with target velocity (Figure 19), so did their size, duration, and peak velocity (Figure 20). Hence, at slow target velocities, a larger number of smaller, slower and briefer saccades were generated to cover the 40.0 deg spatial trajectory, and at fast target speeds a smaller number of larger saccades covered the distance. Overall though, the ratio of saccadic eye movements generated to track jumping-dot motion did not change significantly. When the two ratio measures are directly compared, the distance-based ratio of saccadic versus pursuit eye movements had a tendency to be larger than the time-based ratio (Figure 21), although this did not reach the stringent 0.01 alpha levels due to the large variability in the distance-based ratio data.

Summary of visual tracking of continuous and jumping-dot motion stimuli

Figure 22 displays traces of visual tracking of continuous and jumping-dot motion stimuli, which illustrate the pattern of visual tracking of the two motion stimuli at different target velocities. While dual-mode tracking eye velocity and gain for continuous and jumping-dot motion stimuli were very similar, this is clearly accomplished using different combinations of smooth-pursuit and saccadic eye movements. Dual-mode tracking of continuous motion stimuli consists mainly of smooth pursuit eye movements with occasional small saccades at slower target velocities, and fewer but larger and faster saccades at faster target velocities. In contrast, dual-mode tracking of jumping-dot motion stimuli has a significantly larger saccadic component. At slower target velocities (absolute values depend on the spatial separation) a large number of small saccades track the target, interspersed with small segments of smooth pursuit, and as target speed increases, visual tracking becomes smoother, supplemented by a smaller number of larger, faster and temporally longer saccades.

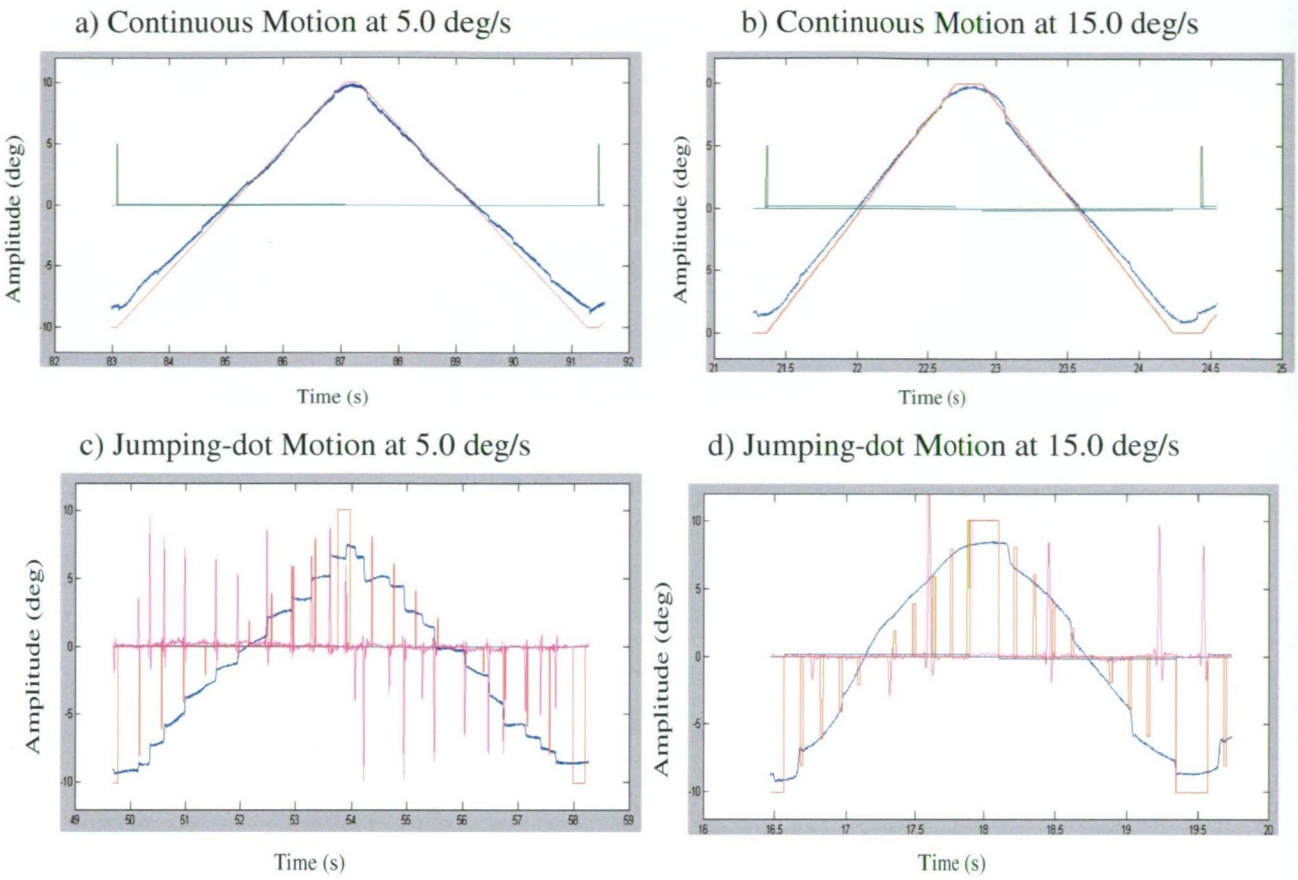

Figure 22. Eye trace (blue line) of one cycle (40.0 deg) of visual tracking for a representative participant (DH) tracking continuous motion (a & b) and jumping-dot motion (c & d) at 5.0 deg/s and 15.0 deg/s target velocity with 2.0 deg spatial separation at 20ms stimulus duration. Red lines represent the continuous or jumping-dot target; the pink line is the velocity trace.

A comparison of visual tracking of continuous and slashed motion stimuli

In order to compare visual tracking of slashed apparent motion stimuli with continuous motion, 2 [Type of Motion: Continuous, Slashed] X 8 [Velocity: 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s] repeated measures ANOVAs were conducted for all dependent variables, for each of the five spatial separations [0.5 deg spatial separation only allowed six target velocities], using Greenhouse-Geisser correction and a Bonferroni-adjusted alpha level of .01. The results are summarised in Table 5 and statistical output files are presented electronically in Appendix H.

Table 5. Summary of main effects and interactions comparing visual tracking of continuous and slashed motion stimuli across target speed for each spatial separation.

Measure	Spatial Separation	Main Effect Type of Motion	Main Effect Velocity	Type of Motion X Velocity Interaction
Dual-Mode Tracking	(deg)			
Dual-Mode Eye Velocity	0.5	$F(1,4)=0.5,\eta^2=.01$	**$F(1,5)=1458.6,\eta^2=1.00$****	$F(1,5)=2.4,\eta^2=.38$
	1.0	$F(1,5)=0.4,\eta^2=.07$	**$F(1,6)=34.8,\eta^2=.87$***	$F(3,15)=3.1,\eta^2=.38$
	2.0	$F(1,5)=0.6,\eta^2=.10$	**$F(1,6)=43.3,\eta^2=.90$***	$F(2,10)=3.3,\eta^2=.40$
	4.0	$F(1,5)=0.5,\eta^2=.08$	**$F(1,7)=54.0,\eta^2=.92$****	$F(2,12)=1.3,\eta^2=.21$
	5.0	$F(1,5)=0.3,\eta^2=.06$	**$F(1,7)=73.9,\eta^2=.94$****	$F(1,7)=1.7,\eta^2=.25$
Dual-Mode Gain	0.5	$F(1,4)=2.8,\eta^2=.41$	$F(2,8)=2.8,\eta^2=.41$	$F(2,8)=1.4,\eta^2=.26$
	1.0	$F(1,5)=5.7,\eta^2=.53$	$F(1,7)=4.1,\eta^2=.45$	$F(3,13)=1.7,\eta^2=.25$
	2.0	**$F(1,5)=27.0,\eta^2=.84$***	$F(1,7)=4.3,\eta^2=.46$	$F(2,11)=0.5,\eta^2=.09$
	4.0	$F(1,5)=8.3,\eta^2=.62$^	$F(1,7)=6.3,\eta^2=.56$^	$F(3,16)=0.8,\eta^2=.13$
	5.0	$F(1,5)=5.3,\eta^2=.52$	$F(2,8)=5.0,\eta^2=.50$^	$F(2,8)=0.7,\eta^2=.13$
Single-Mode Pursuit				
Single-Mode Eye Velocity	0.5	$F(1,4)=2.3,\eta^2=.37$	**$F(1,5)=63.9,\eta^2=.94$***	$F(1,5)=1.9,\eta^2=.33$
	1.0	$F(1,5)=1.3,\eta^2=.21$	**$F(1,5)=18.1,\eta^2=.78$***	$F(2,10)=2.4,\eta^2=.33$
	2.0	$F(1,5)=9.3,\eta^2=.65$^	**$F(1,5)=19.2,\eta^2=.79$***	$F(3,13)=1.6,\eta^2=.25$
	4.0	**$F(1,5)=19.3,\eta^2=.79$***	**$F(1,6)=22.4,\eta^2=.82$***	$F(2,8)=3.7,\eta^2=.43$
	5.0	**$F(1,5)=14.9,\eta^2=.75$***	**$F(1,6)=21.3,\eta^2=.81$***	$F(1,7)=2.6,\eta^2=.34$
Single-Mode Gain	0.5	$F(1,4)=0.0,\eta^2=.00$	$F(1,5)=2.4,\eta^2=.38$	$F(2,8)=5.1,\eta^2=.56$^
	1.0	$F(1,5)=0.5,\eta^2=.01$	$F(1,6)=3.0,\eta^2=.38$	**$F(3,14)=6.3,\eta^2=.56$***
	2.0	$F(1,5)=6.4,\eta^2=.56$	$F(1,6)=4.2,\eta^2=.46$	**$F(3,15)=7.4,\eta^2=.60$***
	4.0	**$F(1,5)=23.6,\eta^2=.83$***	$F(2,9)=4.5,\eta^2=.48$^	**$F(2,12)=9.9,\eta^2=.66$***
	5.0	**$F(1,5)=25.6,\eta^2=.84$***	$F(1,6)=2.6,\eta^2=.35$	**$F(2,12)=10.2,\eta^2=.67$***
Saccades				
Saccade Frequency per second	0.5	$F(1,4)=5.1,\eta^2=.56$	**$F(2,8)=14.5,\eta^2=.78$***	$F(2,6)=1.7,\eta^2=.30$
	1.0	$F(1,5)=4.3,\eta^2=.46$	**$F(2,8)=12.0,\eta^2=.71$***	$F(1,7)=0.5,\eta^2=.10$
	2.0	$F(1,5)=6.9,\eta^2=.58$^	**$F(2,12)=17.2,\eta^2=.76$****	$F(2,10)=3.4,\eta^2=.40$
	4.0	$F(1,5)=9.7,\eta^2=.66$^	**$F(1,7)=18.5,\eta^2=.79$***	$F(1,7)=0.3,\eta^2=.05$
	5.0	**$F(1,5)=20.3,\eta^2=.80$***	**$F(2,11)=21.1,\eta^2=.81$****	$F(2,12)=3.0,\eta^2=.38$
Saccade Frequency per cycle	0.5	$F(1,5)=0.7,\eta^2=.13$	$F(1,6)=8.4,\eta^2=.63$^	$F(2,9)=6.9,\eta^2=.58$^
	1.0	$F(1,5)=2.6,\eta^2=.34$	**$F(2,8)=12.5,\eta^2=.71$***	$F(1,7)=4.3,\eta^2=.46$
	2.0	$F(1,5)=12.1,\eta^2=.71$^	**$F(2,8)=27.6,\eta^2=.85$****	**$F(2,8)=11.3,\eta^2=.69$***
	4.0	$F(1,5)=12.4,\eta^2=.71$^	**$F(1,7)=29.1,\eta^2=.85$***	**$F(1,7)=12.5,\eta^2=.72$***
	5.0	$F(1,5)=13.4,\eta^2=.73$^	**$F(1,6)=18.3,\eta^2=.79$***	**$F(2,10)=13.8,\eta^2=.70$***
Saccade Amplitude	0.5	$F(1,5)=0.6,\eta^2=.10$	$F(1,6)=4.7,\eta^2=.48$	$F(3,14)=1.7,\eta^2=.26$
	1.0	$F(1,5)=1.7,\eta^2=.25$	$F(1,6)=4.9,\eta^2=.50$	$F(2,10)=0.6,\eta^2=.10$
	2.0	$F(1,5)=5.8,\eta^2=.45$	$F(1,7)=4.2,\eta^2=.45$	$F(2,11)=0.3,\eta^2=.05$
	4.0	$F(1,5)=10.0,\eta^2=.67$^	$F(2,8)=7.8,\eta^2=.61$^	$F(1,6)=0.1,\eta^2=.03$
	5.0	$F(1,6)=6.0,\eta^2=.50$^	$F(2,9)=5.7,\eta^2=.49$^	$F(2,10)=1.1,\eta^2=.15$
Saccade Duration	0.5	**$F(1,4)=40.7,\eta^2=.91$***	**$F(1,6)=22.3,\eta^2=.85$***	$F(2,8)=0.4,\eta^2=.09$
	1.0	$F(1,5)=7.5,\eta^2=.60$^	**$F(2,11)=17.3,\eta^2=.78$****	$F(3,14)=1.3,\eta^2=.21$
	2.0	**$F(1,5)=22.2,\eta^2=.82$***	**$F(3,14)=18.8,\eta^2=.75$****	$F(2,12)=1.0,\eta^2=.17$
	4.0	**$F(1,5)=24.6,\eta^2=.83$***	**$F(3,14)=20.8,\eta^2=.81$****	$F(2,12)=1.6,\eta^2=.24$
	5.0	**$F(1,5)=46.2,\eta^2=.90$***	**$F(2,11)=20.0,\eta^2=.80$****	$F(3,13)=2.0,\eta^2=.28$
Saccade Peak Velocity	0.5	$F(1,4)=1.6,\eta^2=.29$	$F(2,7)=7.1,\eta^2=.64$^	$F(2,7)=0.6,\eta^2=.12$
	1.0	$F(1,5)=1.8,\eta^2=.26$	**$F(2,11)=10.2,\eta^2=.67$***	$F(3,13)=0.5,\eta^2=.10$
	2.0	$F(1,5)=2.9,\eta^2=.37$	**$F(2,9)=7.6,\eta^2=.60$***	$F(3,13)=0.3,\eta^2=.06$
	4.0	$F(1,5)=5.2,\eta^2=.51$	**$F(2,12)=13.3,\eta^2=.73$****	$F(1,7)=0.1,\eta^2=.01$
	5.0	$F(1,5)=8.3,\eta^2=.62$^	**$F(2,9)=12.1,\eta^2=.71$***	$F(2,9)=0.7,\eta^2=.12$
	0.5	$F(1,4)=0.5,\eta^2=.11$	**$F(1,5)=20.9,\eta^2=.84$***	$F(2,6)=0.7,\eta^2=.15$
Time-based	1.0	$F(1,5)=0.2,\eta^2=.03$	**$F(1,7)=22.9,\eta^2=.82$***	$F(1,7)=0.3,\eta^2=.06$
Saccade Ratio	2.0	$F(1,5)=3.3,\eta^2=.40$	**$F(2,9)=19.6,\eta^2=.80$***	$F(2,8)=0.7,\eta^2=.12$
	4.0	$F(1,5)=4.1,\eta^2=.45$	**$F(1,7)=22.2,\eta^2=.82$***	$F(1,6)=0.7,\eta^2=.12$
	5.0	$F(1,5)=5.0,\eta^2=.50$	**$F(2,11)=27.0,\eta^2=.84$****	$F(1,7)=0.5,\eta^2=.08$
Distance-based	0.5	$F(1,4)=2.0,\eta^2=.33$	$F(1,5)=1.8,\eta^2=.32$	$F(2,6)=1.6,\eta^2=.28$
Saccade Ratio	1.0	$F(1,5)=1.5,\eta^2=.23$	$F(1,5)=2.3,\eta^2=.32$	$F(1,5)=1.0,\eta^2=.17$
	2.0	$F(1,5)=6.2,\eta^2=.55$	$F(1,6)=3.3,\eta^2=.40$	$F(1,7)=1.5,\eta^2=.23$
	4.0	$F(1,5)=12.7,\eta^2=.72$^	$F(1,6)=1.1,\eta^2=.18$	$F(1,7)=1.2,\eta^2=.20$
	5.0	**$F(1,5)=16.3,\eta^2=.77$***	$F(1,6)=1.3,\eta^2=.20$	$F(1,7)=1.3,\eta^2=.20$

Note: ^.05>*p*>.01; **p*<.01, ***p*<.001; significant effects are in bold.

Dual-mode tracking of slashed motion stimuli

There were generally no significant differences in dual-mode eye velocity or gain for continuous and slashed motion (Table 5), with the only exception that participants had significantly lower dual-mode gain for slashed compared to continuous motion at 2.0 deg spatial separation, an effect which was close to significance for the jumping-dot stimuli (p=.02). As expected, dual-mode eye velocity increased significantly with increasing target velocity for both types of motion, to keep up with the target stimulus (Figure 23a), but dual-mode gain for was not affected by target velocity (Figure 23b). The finding that dual-mode tracking gain was not affected by the type of motion, target velocity, and spatial separation demonstrates how accurate visual tracking is when saccadic and smooth pursuit eye movements track together, even when the target is a highly degraded slashed motion stimulus.

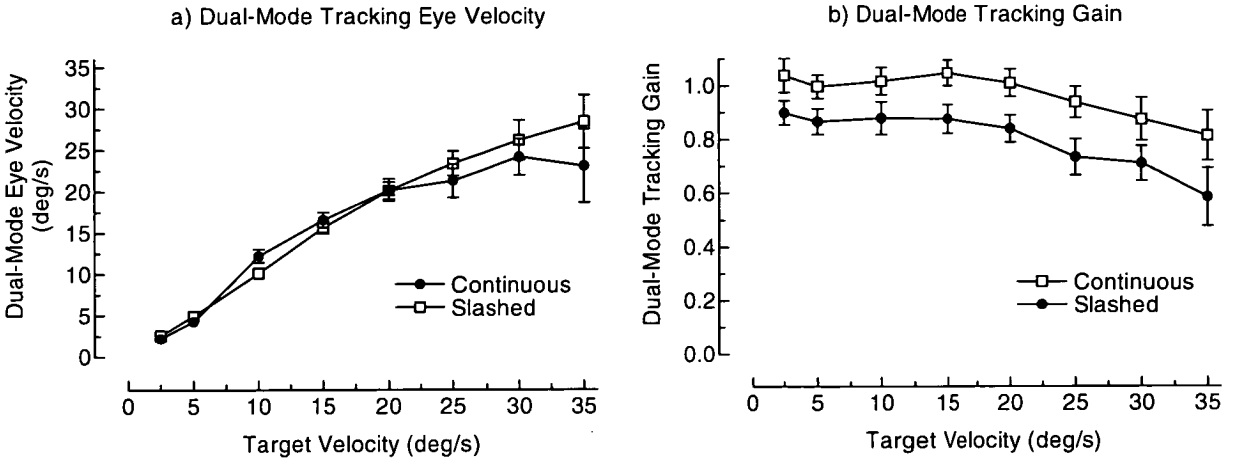

Figure 23. Dual-mode (a) eye velocity and (b) gain in response to continuous and slashed motion (averaged for spatial separation). Error bars depict standard error of the mean (*SE*).

Single-mode pursuit of slashed motion stimuli

As expected, single-mode pursuit eye velocity increased significantly with increasing target velocity (Table 5). For small spatial separations (0.5-2.0 deg) there was no difference in single-mode eye velocity for continuous and slashed motion, but for spatial separations of 4.0 and 5.0 deg, single-mode pursuit eye velocity was significantly faster when tracking continuous than slashed motion stimuli (see Figure 24).

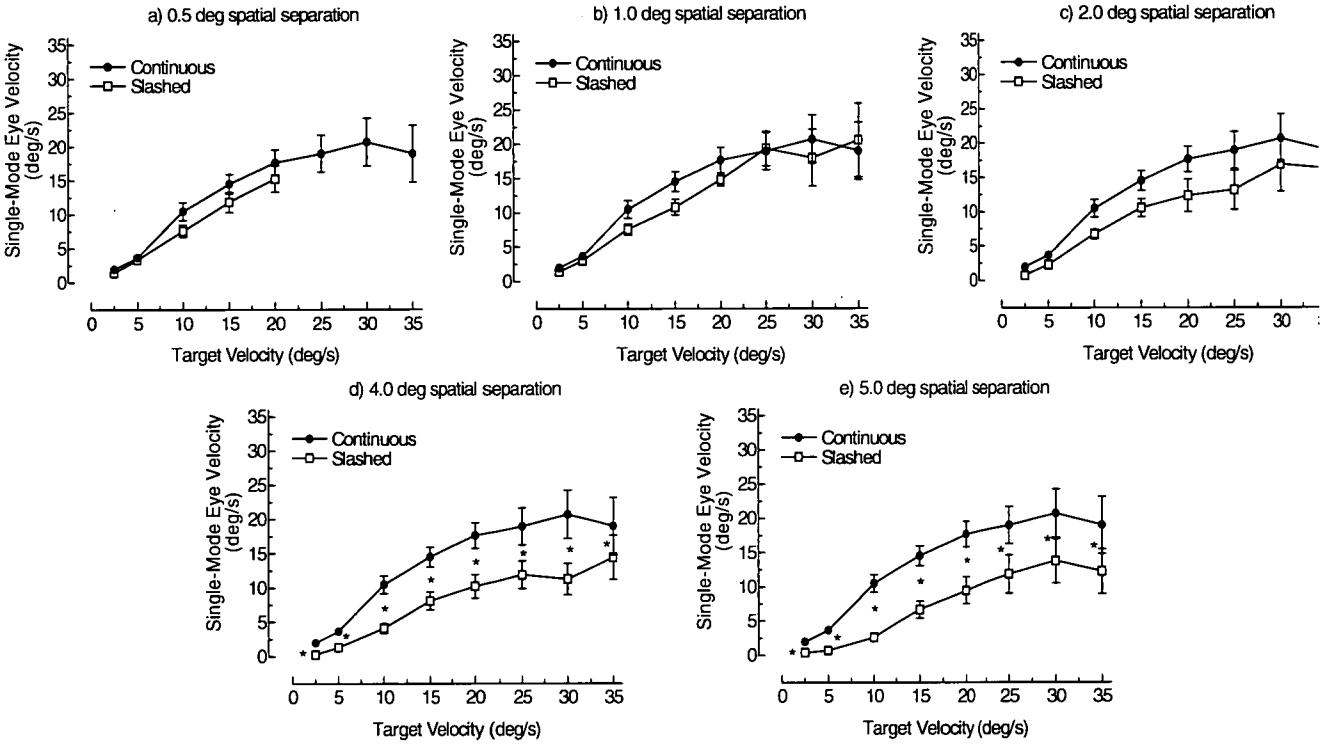

Figure 24. Single-mode eye velocity in response to continuous and slashed motion as a function of target velocity for each spatial separation (* denote significant differences, $p<.01$; error bars depict *SE*). A linear increase in single-mode eye velocity was evident for continuous [$F(1,6)=28.0$, $p<.01$,$\eta^2=.82$], and slashed motion for spatial separations: (a) 0.5 deg [$F(1,4)=55.6$, $p<.01$, $\eta^2=.93$], (b) 1.0 deg [$F(1,5)=18.5$,$p<.01$, $\eta^2=.78$], (c) 2.0 deg [$F(1,5)=15.7$,$p<.01$, $\eta^2=.76$], (d) 4.0 deg [$F(1,5)=21.6$,$p<.01$,$\eta^2=.81$], and (e) 5.0 deg [$F(1,4)=14.3$,$p<.05$, $\eta^2=.74$].

There was no difference in single-mode pursuit gain for continuous and slashed motion when spatial separations were small (0.5-2.0 deg), but single-mode pursuit gain was significantly higher for continuous than for slashed motion at 4.0 and 5.0 deg spatial separation. Consistent with the findings for jumping-dot motion, the interaction between type of motion and target velocity was significant for spatial separations greater than 0.5 deg (Table 5). As illustrated in Figure 25, single-mode pursuit in response to continuous and slashed motion exhibited a strikingly different pattern as a function of target velocity. Single-mode pursuit gain elicited by continuous motion decreased linearly with increasing target velocity, but pursuit gain for slashed motion showed a quadratic pattern. Similar to the results for jumping-dot motion, single-mode pursuit gain elicited by slashed motion stimuli was low at both slow and fast target velocities, with peak pursuit performance at moderate velocities (depending on spatial separation). Pairwise comparisons showed that the largest differences in single-mode pursuit gain for continuous and slashed motion at 2.0-5.0 deg spatial separation were slow target velocities, while at faster target velocities smooth pursuit of continuous and slashed motion was very similar.

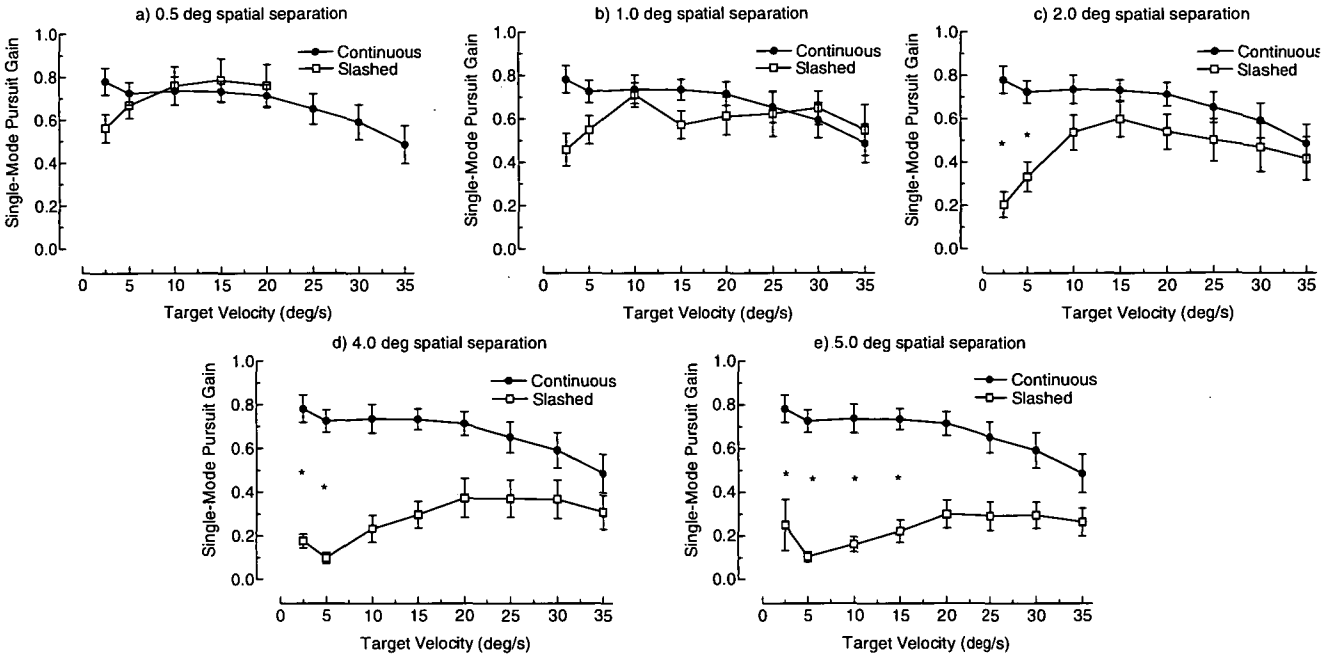

Figure 25. Single-mode pursuit gain elicited by continuous and slashed motion stimuli as a function of target velocity for each spatial separation (* denote significant differences, $p<.01$; error bars depict *SE*). Single-mode pursuit gain to continuous motion decreased linearly [$F(1,6)=9.3, p<.05, \eta^2=.55$], while single-mode pursuit gain for slashed motion followed nonlinear trends: (a) 0.5: no significant trend, (b) 1.0 deg: quadratic $F(1,5)=23.5, p<.01, \eta^2=.83$, (c) 2.0 deg: quadratic $F(1,5)=33.9, p<.01, \eta^2=.87$, (d) 4.0 deg: quadratic $F(1,5)=30.1, p<.01, \eta^2=.86$), and (e) 5.0 deg: cubic $F(1,5)=12.6, p<.05, \eta^2=.72$.

An examination of the quadratic function for single-mode pursuit gain in response to slashed motion as a function of target velocity in Figure 25 shows that the peak performance of single-mode pursuit gain was located at different target velocities for different spatial separations. For spatial separations of 0.5-2.0 deg highest pursuit gain was at target velocities of 10.0-15.0 deg/s, but for 4.0 and 5.0 deg spatial separation peak gain was at 20.0-30.0 deg/s target speed. This indicates that peak single-mode pursuit gain in response to slashed motion shifts to faster target velocities when spatial separation is increased.

Main sequence relationship of saccades elicited by slashed motion stimuli

The main sequence relationships for all saccades generated in the tracking of slashed motion are displayed in Figure 26. The saccades present in the tracking of slashed motion follow the general linear main sequence relationship that has been described for saccades in response to stationary and continuously moving targets (De Brouwer, Missal et al., 2002; Experiment 1), which indicates that saccades occurring in the tracking of apparent motion have the same general dynamics and presumably the same underlying mechanisms as saccades in response to continuous motion and stationary targets.

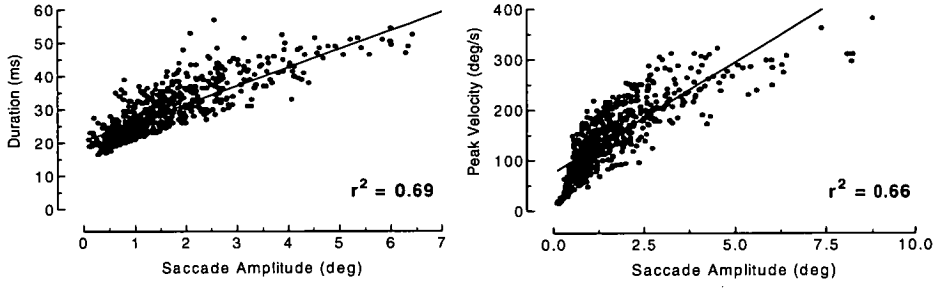

Figure 26. Main sequence relationship between mean saccade amplitude and mean saccade duration and peak velocity for saccades generated in the tracking of all combinations of spatial separation and target velocity for slashed motion stimuli.

Frequency of saccades elicited by slashed motion stimuli

As summarised in Table 5 and illustrated in Figures 27 and 28, saccade frequency per second and per cycle showed distinct patterns with increasing target velocity. The number of saccades generated per second increased significantly with increasing target velocity in response to both continuous and slashed motion (Figure 27). The differences between the two types of motion reached statistical significance only for 5.0 deg spatial separation and shows that significantly more saccades were produced per second in the tracking of slashed motion at all target velocities

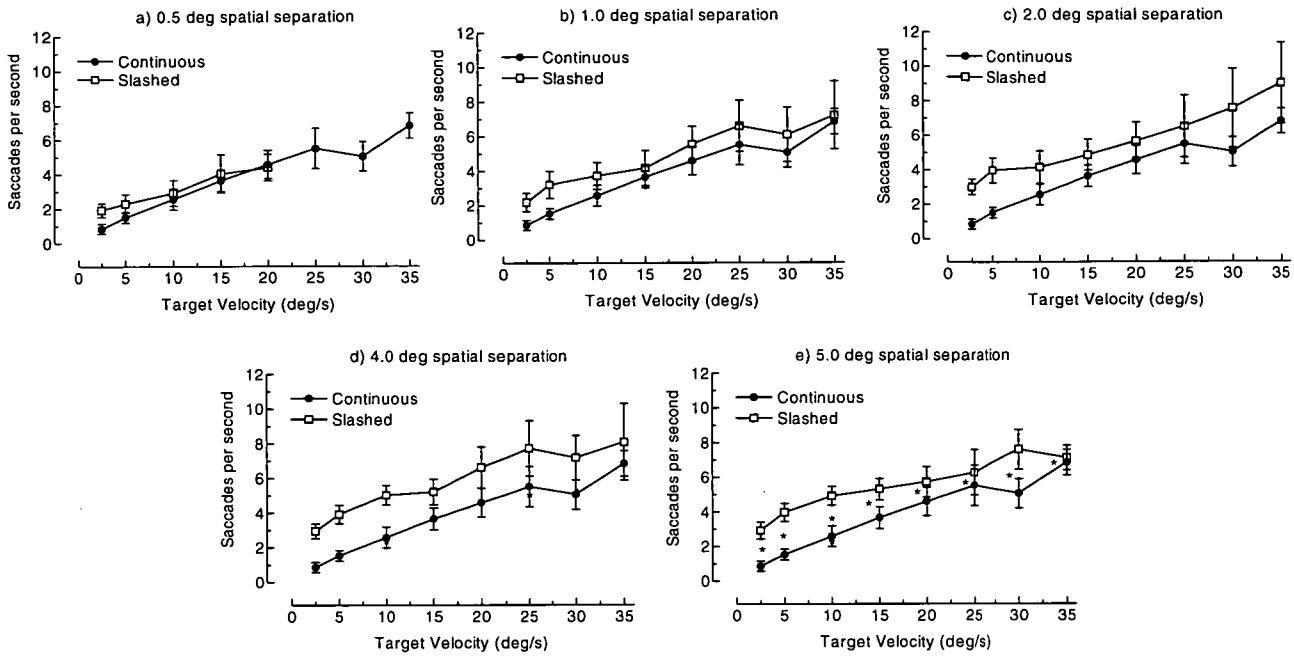

Figure 27. Saccade frequency per second for continuous and slashed motion for each spatial separation (* denote significant differences between types of motion, $p<.01$; error bars depict *SE*).

Consistent with findings for jumping-dot motion, the number of saccades per cycle (per 40.0 deg of tracking) decreased with increasing target velocity (see Figure 28). The interaction between the type of motion and target velocity was only significant for spatial separations of 2.0 deg and more. Pairwise comparisons revealed that more saccades per spatial unit were generated when tracking slashed motion compared to continuous motion, but only for very slow target velocities (2.5-5.0 deg/s, depending on spatial separation), with no differences at faster target velocities even for large spatial separations.

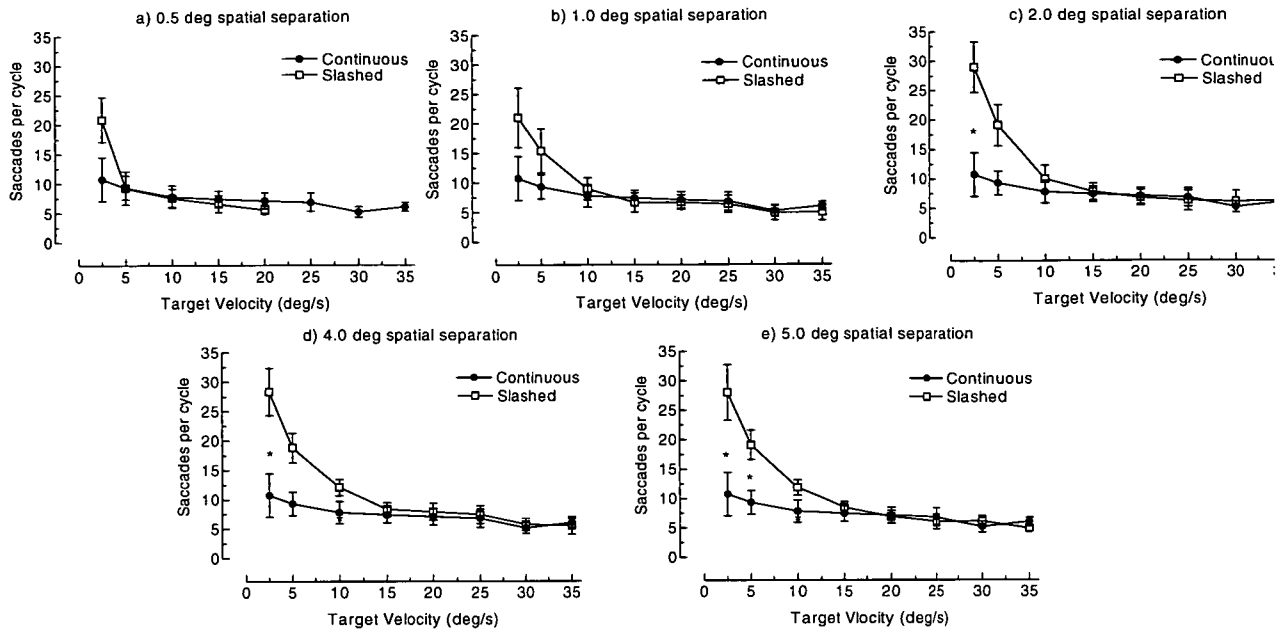

Figure 28. Saccade frequency per cycle for continuous and slashed motion for each spatial separation, with significant interaction between type of motion and target velocity for slash separations of 2.0, 4.0 and 5.0 deg (* denote significant differences between types of motion, $p<.006$; error bars depict *SE*).

Characteristics of saccades elicited by slashed motion stimuli

For both continuous and slashed motion saccades became increasingly faster and of longer duration with increasing target velocity (Table 5), which is illustrated in Figure 29. The main effect of target velocity on saccade amplitude (corrected for pursuit velocity) did not reach significance when tracking slashed motion, although it was significant when saccade amplitude was not corrected for pursuit velocity. This means that although the absolute saccade amplitude increased with pursuit velocity, this effect was no longer significant when the pursuit eye velocity component was removed (De Brouwer, Missal et al., 2002), which suggests that this increase in saccade size at faster target speeds may be due to pursuit dynamics added to saccadic eye movements.

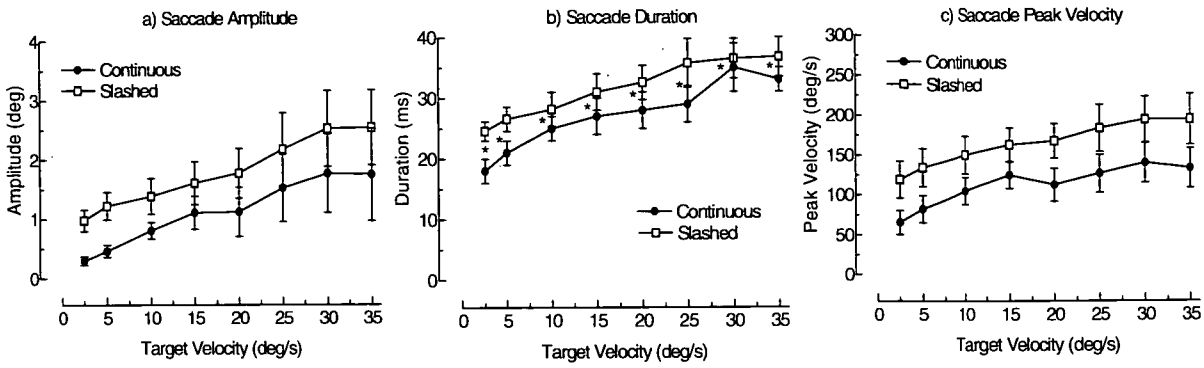

Figure 29. Saccade characteristics in response to continuous and slashed motion for (a) saccade amplitude (b) duration and (c) peak velocity as a function of target velocity (averaged for spatial separation). * denote significant differences ($p<.01$); error bars depict *SE*.

Ratio of saccadic versus smooth pursuit eye movements in the visual tracking of slashed motion stimuli

The ratio of saccadic versus pursuit eye movements elicited by slashed motion exhibited very similar functional patterns as found for jumping-dot motion. There was no difference between continuous and slashed motion with regard to the time-based and distance-based ratio of saccades versus pursuit. As illustrated in Table 5 and Figure 30, the distance-based ratio of saccadic eye movements had a tendency to be larger than for continuous motion, but only reached the stringent 0.01 significance level at 5.0 deg slash separation due to the large variability in the data (see large *SE* in Figure 30b). The duration of time spent in saccadic eye movements increased significantly and linearly [$F(1,4)=17.1, p<.05, \eta^2=.81$] with increasing target velocity, and for both continuous and slashed motion there were more saccades per second with increasing target velocity (Figure 27). However, as outlined in Chapter 6, time-based measures are affected by the differences in dynamics of saccadic and smooth pursuit eye movements, as well as overall tracking time and are therefore not very accurate measures to estimate the saccadic tracking component.

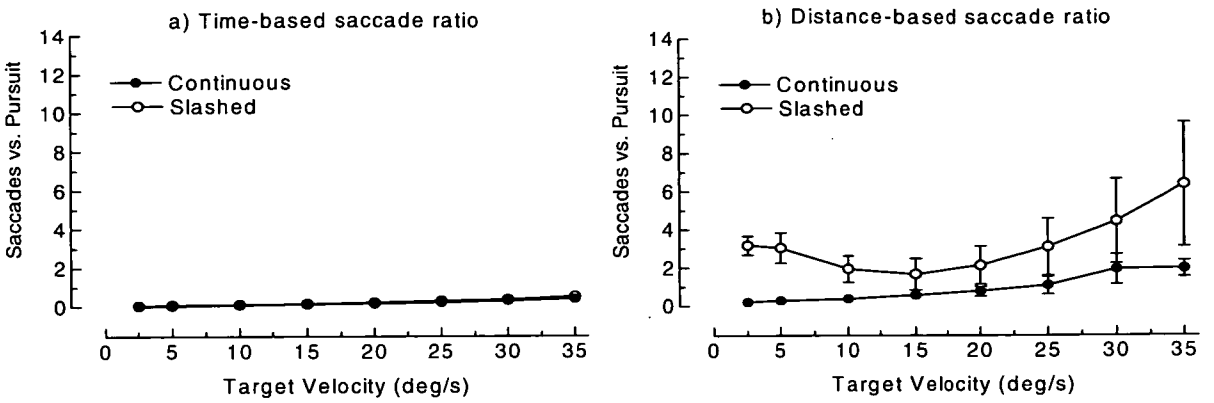

Figure 30. Ratio of (a) duration and (b) spatial distance of saccadic versus pursuit eye movements in the tracking of continuous and slashed motion (averaged for spatial separation; error bars depict *SE*).

Consistent with the findings for jumping-dot motion, the main effect of target speed on the distance-based ratio data was not significant for slashed motion, but it followed a significant quadratic trend [$F(1,4)=7.3$, $p=.05$, $\eta^2=.65$], with a larger saccadic contribution to visual tracking at both slow and fast target speeds (see Figure 30b). The nature of this saccadic tracking component differs at slow and fast target speeds: at slow target velocities a larger number of slower and briefer saccades were produceded to cover the 40.0 deg spatial trajectory and at fast target speeds a smaller number of saccades are generated, but these are of longer duration, faster, and larger (when amplitude was not corrected for pursuit velocity) (Figures 28 and 29). Also, the ratio of saccades versus pursuit eye movements was larger when estimated based on distance, rather than time (Figure 30), but the significance levels did not reach the stringent 0.01 alpha levels due to the large variability in the distance-based ratio data.

Summary of visual tracking of slashed apparent motion

Figure 31 displays examples of eye traces of visual tracking of continuous and slashed motion stimuli, and this illustrates the pattern of visual tracking elicited by slashed motion at different target speeds. While dual-mode tracking eye velocity and

gain in response to both continuous and slashed motion are very similar, this is clearly accomplished using different combinations of smooth-pursuit and saccadic eye movements. Dual-mode tracking of continuous motion stimuli consists mainly of smooth pursuit eye movements, with occasional small saccades at slower target velocities, and fewer but larger and faster saccades at faster target velocities. In contrast, dual-mode tracking of slashed motion stimuli has a significantly larger saccadic component. At slower target velocities (absolute values depend on the spatial separation) a large number of small saccades track the target, interspersed with small segments of smooth pursuit, and as target speed increases, visual tracking becomes smoother, supplemented by a smaller number of larger, faster and temporally longer saccades.

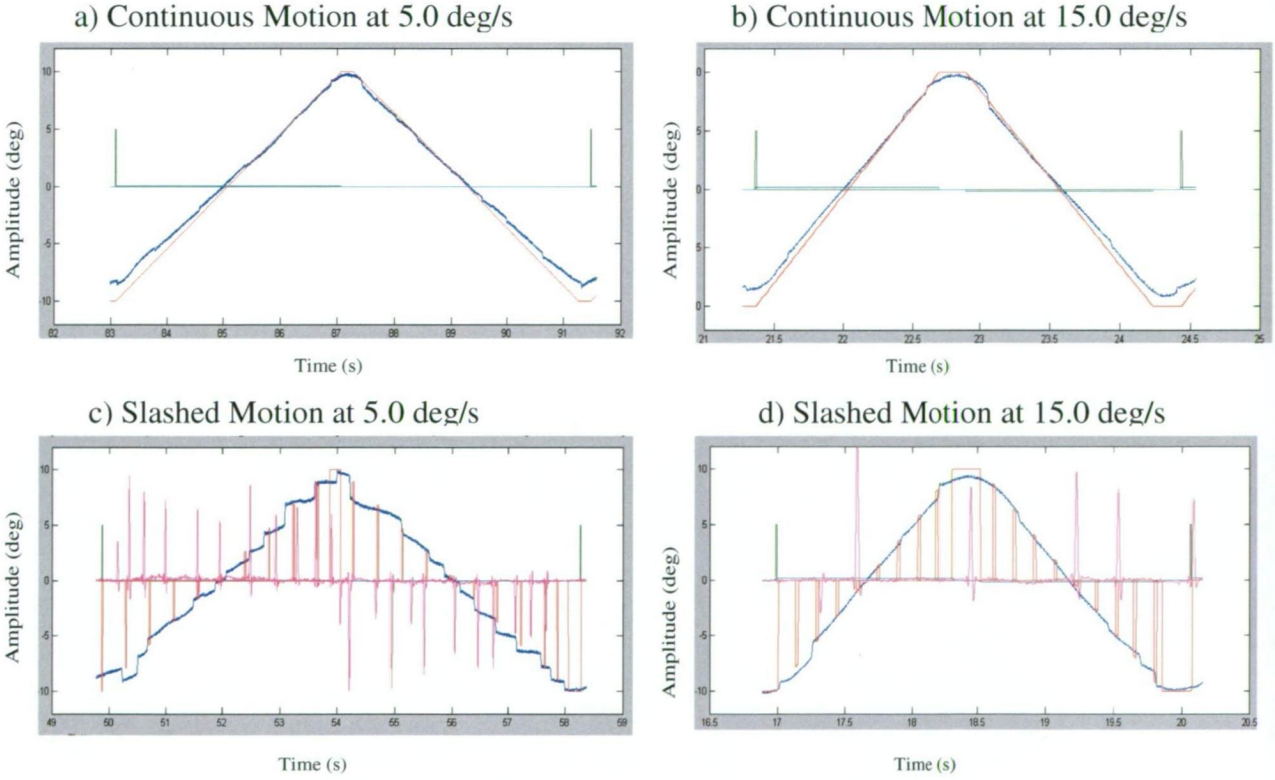

Figure 31. Eye trace (blue line) of one cycle (40.0 deg) of visual tracking for a representative participant (DH) tracking continuous motion (a & b) and slashed motion (c & d) at 5.0 deg/s and 15.0 deg/s target velocity with 2.0 deg spatial separation at 20ms stimulus duration. Red lines represent the continuous or jumping-dot target; the pink line is the velocity trace.

The effects of spatial separation on the visual tracking of apparent motion stimuli

The comparisons of visual tracking of continuous and apparent motion reported so far were conducted separately for each spatial separation, for ease of analysis and interpretation. As can be seen in Tables 4 and 5, the differences between continuous and apparent motion stimuli were not significant for small spatial separations, but this was statistically examine conducting a 5 [Spatial Separation: 0.5, 1.0, 2.0, 4.0, 5.0 deg] X 6 [Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0 deg/s] ANOVA and a 4 [Spatial Separation: 1.0, 2.0, 4.0, 5.0 deg] X 9 [Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s] ANOVA for each dependent variable (Bonferroni-adjusted α=.025) separately for jumping-dot and slashed motion. While this resulted in some overlap and redundancy in the data, it ensured that the whole range of target speeds at each spatial separation was analysed. The results for the effects of spatial separation are summarised in Table 6 for jumping-dot motion and Table 7 for slashed motion (output files are presented electronically in Appendices I and J). The main effects for target velocity were not reported again because velocity effects have been reported previously (see Tables 4 and 5).

Table 6. Main effects and interactions for spatial separation on the visual tracking of

Measure	Analysis of Variance	Main Effect of Spatial Separation	Spatial Separation X Velocity Interaction
Dual-Mode Tracking			
Dual-Mode Eye	5 X 6	$F(1,8)=3.2,\eta^2=.35$	$F(3,15)=1.6,\eta^2=.21$
Velocity	4 X 9	$F(1,9)=5.9,\eta^2=.50$^	$F(2,14)=1.2,\eta^2=.16$
Dual-Mode Gain	5 X 6	$F(1,9)=3.8,\eta^2=.39$	$F(4,27)=1.2,\eta^2=.17$
	4 X 9	$F(1,9)=5.8,\eta^2=.49$^	$F(3,18)=0.8,\eta^2=.11$
Single-Mode Pursuit			
Single-Mode Eye	5 X 6	**$F(2,11)=43.1,\eta^2=.89$*****	**$F(3,18)=8.3,\eta^2=.58$****
Velocity	4 X 9	**$F(1,8)=27.5,\eta^2=.82$*****	**$F(3,21)=5.2,\eta^2=.46$****
Single-Mode Gain	5 X 6	**$F(2,10)=41.8,\eta^2=.88$*****	**$F(4,22)=4.8,\eta^2=.45$****
	4 X 9	**$F(1,8)=31.1,\eta^2=.84$*****	**$F(4,24)=3.5,\eta^2=.37$****
Saccades			
Saccade Frequency	5 X 6	**$F(2,9)=7.2,\eta^2=.55$***	$F(4,22)=2.3,\eta^2=.28$
per second	4 X 9	**$F(2,13)=14.0,\eta^2=.70$****	$F(5,28)=1.9,\eta^2=.24$
Saccade Frequency	5 X 6	$F(1,8)=4.5,\eta^2=.43$	$F(3,15)=2.8,\eta^2=.32$
per cycle	4 X 9	$F(2,12)=5.0,\eta^2=.46$^	$F(3,18)=2.9,\eta^2=.33$
Saccade Amplitude	5 X 6	**$F(1,7)=14.6,\eta^2=.71$****	$F(4,23)=1.0,\eta^2=.15$
	4 X 9	**$F(2,10)=12.2,\eta^2=.67$****	$F(2,12)=1.2,\eta^2=.16$
Saccade Duration	5 X 6	**$F(2,13)=21.3,\eta^2=.78$*****	$F(3,18)=1.2,\eta^2=.17$
	4 X 9	**$F(2,13)=12.5,\eta^2=.68$****	$F(3,18)=1.3,\eta^2=.18$
Saccade Peak Velocity	5 X 6	$F(1,7)=1.1,\eta^2=.15$	$F(4,21)=0.7,\eta^2=.11$
	4 X 9	$F(1,7)=0.9,\eta^2=.13$	$F(3,17)=0.6,\eta^2=.09$
Time-based	5 X 6	**$F(2,10)=10.9,\eta^2=.64$****	$F(3,18)=2.8,\eta^2=.32$
Saccade Ratio	4 X 9	**$F(2,14)=12.5,\eta^2=.68$****	$F(3,18)=3.4,\eta^2=.36$^
Distance-based	5 X 6	**$F(1,8)=25.0,\eta^2=.81$****	$F(3,17)=2.5,\eta^2=.29$
Saccade Ratio	4 X 9	**$F(1,7)=13.0,\eta^2=.68$****	$F(2,10)=1.5,\eta^2=.20$

Note: **5x6:** 5(Spatial Separation: 0.5, 1.0, 2.0, 4.0, 5.0 deg) X 6 (Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0 deg/s), **4x9**: 4 (Spatial Separation: 1.0, 2.0, 4.0, 5.0 deg) X 9 (Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s). ^.05>p>.025, *p<.025, **p<.01, ***p<.001; significant effects are in bold.

jumping-dot motion stimuli

Table 7. Main effects and interactions for spatial separation in the visual tracking of slashed motion stimuli

Measure	Analysis of Variance	Main Effect of Spatial Separation	Spatial Separation X Velocity Interaction
Dual-Mode Tracking			
Dual-Mode Eye	5 X 6	$F(2,9)=0.9,\eta^2=.19$	$F(3,13)=1.3,\eta^2=.25$
Velocity	4 X 9	$F(2,8)=0.2,\eta^2=.03$	$F(2,12)=0.7,\eta^2=.13$
Dual-Mode Gain	5 X 6	$F(2,8)=0.6,\eta^2=.14$	$F(3,1)=0.8,\eta^2=.17$
	4 X 9	$F(2,11)=0.4,\eta^2=.0.7$	$F(3,16)=0.9,\eta^2=.15$
Single-Mode Pursuit			
Single-Mode Eye	5 X 6	**$F(2,7)=19.3,\eta^2=.83$****	$F(3,14)=2.9,\eta^2=.42$
Velocity	4 X 9	**$F(2,8)=11.6,\eta^2=.70$****	$F(3,14)=2.6,\eta^2=.46$
Single-Mode Gain	5 X 6	**$F(2,7)=29.5,\eta^2=.88$****	$F(3,12)=3.0,\eta^2=.43$
	4 X 9	**$F(2,8)=22.7,\eta^2=.82$****	**$F(4,20)=3.5,\eta^2=.42$***
Saccades			
Saccade Frequency	5 X 6	$F(2,7)=1.4,\eta^2=.25$	$F(3,11)=1.1,\eta^2=.21$
per second	4 X 9	$F(2,7)=1.3,\eta^2=.20$	$F(2,12)=1.0,\eta^2=.17$
Saccade Frequency	5 X 6	$F(2,9)=3.3,\eta^2=.40$	$F(3,15)=2.5,\eta^2=.34$
per cycle	4 X 9	$F(1,6)=2.1,\eta^2=.29$	$F(2,12)=2.1,\eta^2=.30$
Saccade Amplitude	5 X 6	**$F(2,9)=26.7,\eta^2=.84$*****	$F(3,13)=1.2,\eta^2=.19$
	4 X 9	$F(1,6)=4.9,\eta^2=.50$	$F(2,9)=1.0,\eta^2=.17$
Saccade Duration	5 X 6	**$F(2,9)=25.0,\eta^2=.86$*****	$F(2,8)=1.3,\eta^2=.24$
	4 X 9	**$F(2,8)=7.0,\eta^2=.58$***	$F(3,14)=0.8,\eta^2=.14$
Saccade Peak Velocity	5 X 6	**$F(1,7)=10.7,\eta^2=.73$***	$F(3,13)=0.6,\eta^2=.14$
	4 X 9	$F(1,6)=2.7,\eta^2=.35$	$F(3,13)=0.8,\eta^2=.14$
Time-based	5 X 6	$F(2,7)=4.5,\eta^2=.53$	$F(3,10)=0.9,\eta^2=.18$
Saccade Ratio	4 X 9	$F(1,6)=4.8,\eta^2=.49$	$F(2,11)=1.3,\eta^2=.21$
Distance-based	5 X 6	**$F(2,8)=17.0,\eta^2=.81$****	$F(2,9)=1.6,\eta^2=.29$
Saccade Ratio	4 X 9	**$F(2,9)=22.8,\eta^2=.82$*****	$F(2,8)=1.5,\eta^2=.23$

Note: **5x6:** 5(Spatial Separation: 0.5, 1.0, 2.0, 4.0, 5.0 deg) X 6 (Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0 deg/s), **4x9**: 4 (Spatial Separation: 1.0 2.0, 4.0, 5.0 deg) X 9 (Target Velocity: 2.5, 5.0, 7.5, 10.0, 15.0, 20.0, 25.0, 30.0, 35.0 deg/s). ^.05>p>.025, *p<.025, **p<.01, ***p<.001; significant effects are in bold.

Dual-mode tracking of jumping-dot motion as a function of spatial separation

Dual-mode tracking was not affected by spatial separation (Table 6), which again highlights that together, smooth pursuit and saccadic eye movements can track a highly degraded apparent motion stimulus with spatial separations as large as 5.0 deg, equally as well as a continuously moving stimulus.

Single-mode pursuit of jumping-dot motion as a function of spatial separation

Single-mode pursuit eye velocity and gain elicited by jumping-dot motion were both affected by spatial separation (Table 6). There was also a significant interaction between spatial separation and target velocity for both single-mode eye velocity and gain. These were followed-up with separate ANOVAs comparing the effects of spatial separation separately for each target velocity (α=.008 and .006), followed by pairwise comparisons. As illustrated in Figure 32, spatial separation did not have a significant effect on single-mode pursuit eye velocity and gain at 2.5 deg/s target velocity, but at faster target velocities increasing spatial separations resulted in significantly slower pursuit eye velocity and significantly lower pursuit gain. Pairwise comparisons between the different spatial separations indicated that the most significant decreases (with largest effect sizes) in eye velocity and pursuit gain were associated with increases in spatial separation from 1.0 to 2.0 deg and from 2.0 to 4.0 deg.

An examination of the interaction between spatial separation and target velocity for single-mode pursuit gain revealed another important finding: the quadratic function for single-mode pursuit gain peaked at different target velocities depending on the spatial separation of the jumping-dot target (see Figure 32 c and d). For small spatial

separations (0.5-2.0 deg) single-mode pursuit gain peaked at target speeds of 10.0-15.0 deg/s, while for larger spatial separations (4.0-5.0 deg) highest single-mode pursuit gain was reached at target velocities of 20.0-30.0 deg/s. This indicates that optimal performance of smooth pursuit eye movements in response to jumping dot motion occurs at faster velocities when the spatial separation between targets increases.

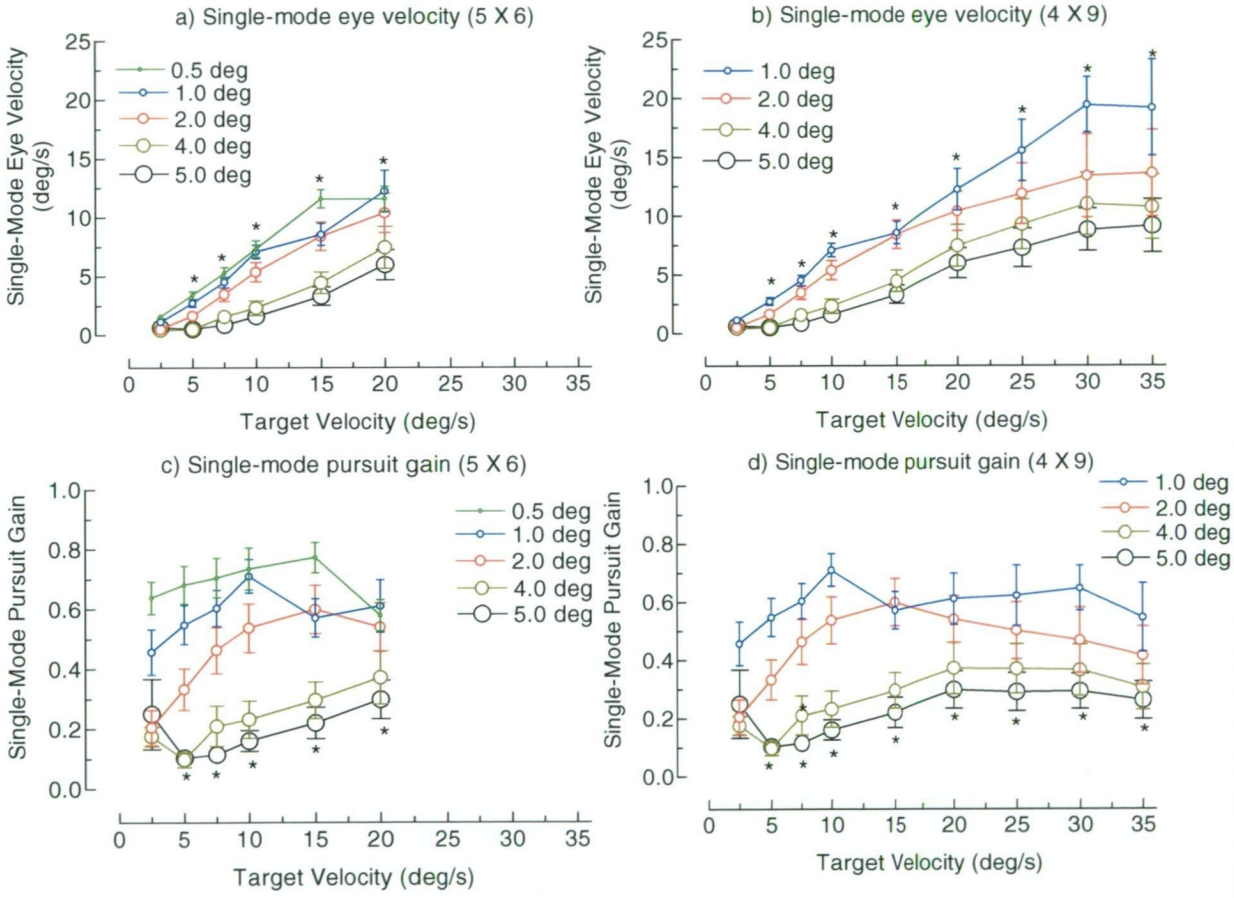

Figure 32. Interaction between spatial separation and target velocity for single-mode pursuit eye velocity (a and b) and gain (c and d) elicited by jumping-dot motion stimuli (error bars depict *SE*; * denote significant effects of spatial separation, $p<.005$, significant spatial steps from 1.0 to 2.0 deg and from 2.0 to 4.0 deg spatial separation).

Saccade frequency and characteristics for jumping-dot motion stimuli as a function of spatial separation

The number of saccades made per second increased significantly with increasing spatial separation (Figure 33), but the trend for a higher number of saccades per cycle did not reach significance (Table 6). Saccade amplitude and saccade duration also increased significantly with increasing spatial separation (see Figure 33), but saccade peak velocity was not affected.

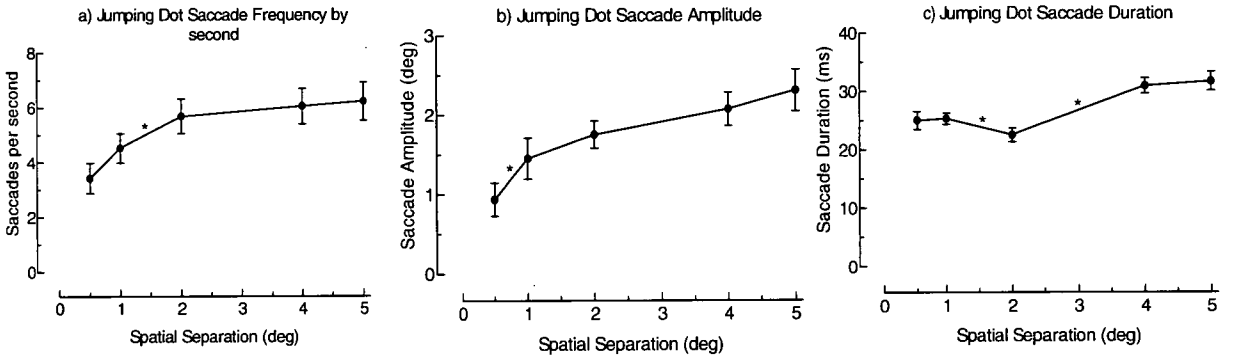

Figure 33. Main effect of spatial separation on (a) saccade frequency per second, (b) saccade amplitude and (c) saccade duration (* denote significant differences, $p<.0125$; error bars depict *SE*).

Ratio of saccadic versus smooth pursuit eye movements for jumping-dot motion stimuli as a function of spatial separation

Both time- and distance-based ratios of saccadic versus pursuit eye movements increased linearly with increasing spatial separation (see Figure 34). It is important to note that the ratio of saccadic versus pursuit eye movements was considerably larger with regard to spatial distance covered, than with regard to time. Saccades covered a substantial part of the spatial trajectory (3:4 ratio of saccades versus pursuit) even when spatial separation was only 0.5 deg, and for spatial separations exceeding 1.0

deg, saccades covered the majority of the spatial trajectory. In contrast, the time-based ratio measure would suggest that even when spatial separation is 5.0 deg, less than a quarter of time is spent in saccadic eye movements, which is inconsistent with the findings of other measures. This provides further support for the view that the distance-based measure is more valid.

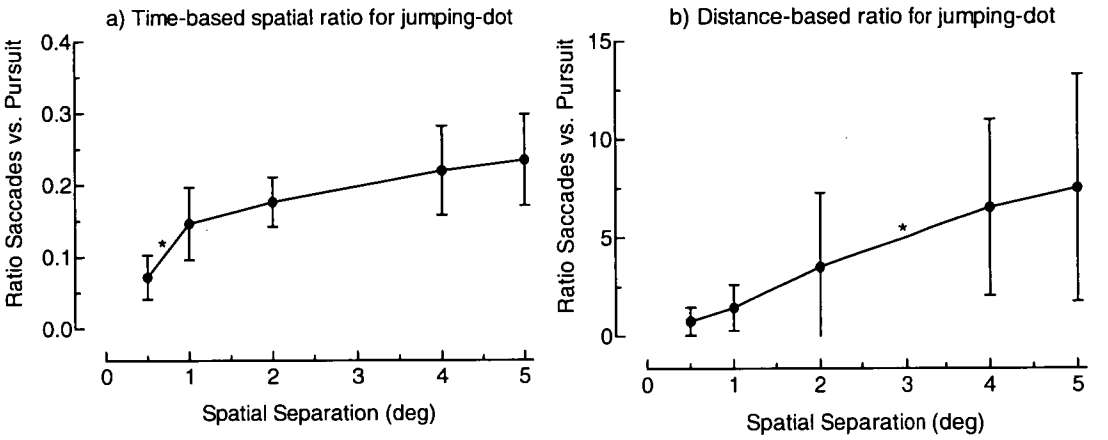

Figure 34. (a) Time-based and (b) distance-based ratio of saccadic versus smooth pursuit eye movement in the tracking of jumping-dot motion (* denote significant differences, p<.0125; error bars depict *SE*). A linear trend was significant for both time-based [$F(1,4)=29.7, p<.01, \eta^2=.88$] and distance-based [$F(1,6)=13.4, p<.05, \eta^2=.69$] ratio. Note that the two figures are on different scales.

Dual-mode tracking of slashed motion as a function of spatial separation

Dual-mode eye velocity and gain for slashed motion were not affected by spatial separation (Table 7), which shows that together smooth pursuit and saccadic eye movements can track a highly degraded apparent motion target, with spatial separations as large as 5.0 deg, equally well as a continuously moving target.

Single-mode pursuit of slashed motion as a function of spatial separation

Single-mode pursuit eye velocity and gain in response to slashed motion were affected by spatial separation (Table 7), as illustrated in Figure 35. Single-mode pursuit eye velocity and gain decreased with increasing spatial separation, with largest effects size associated with an increase in spatial separation from 4.0 to 5.0 deg. There was a significant interaction between spatial separation and target velocity for single-mode pursuit gain, which was followed up with separate ANOVAs comparing the effects of spatial separation separately for each target velocity (α=.008 and .006), followed by pairwise comparisons. These analyses revealed that the effects of spatial separation were not significant for fast target velocities (30.0-35.0 deg/s).

The interaction between spatial separation and target velocity for single-mode pursuit gain revealed another important finding: the quadratic function for single-mode pursuit gain peaked at different target velocities, depending on the spatial separation of the slashed motion target (see Figure 35 c and d). For small spatial separations (0.5-2.0 deg) single-mode pursuit gain peaked at target speeds of 10.0-15.0 deg/s, while for larger spatial separations (4.0-5.0 deg) highest single-mode pursuit gain was reached at target velocities of 15.0-25.0 deg/s. This indicates that optimal performance of smooth pursuit eye movements in response to slashed motion occurs at faster velocities when the spatial separation between targets increases.

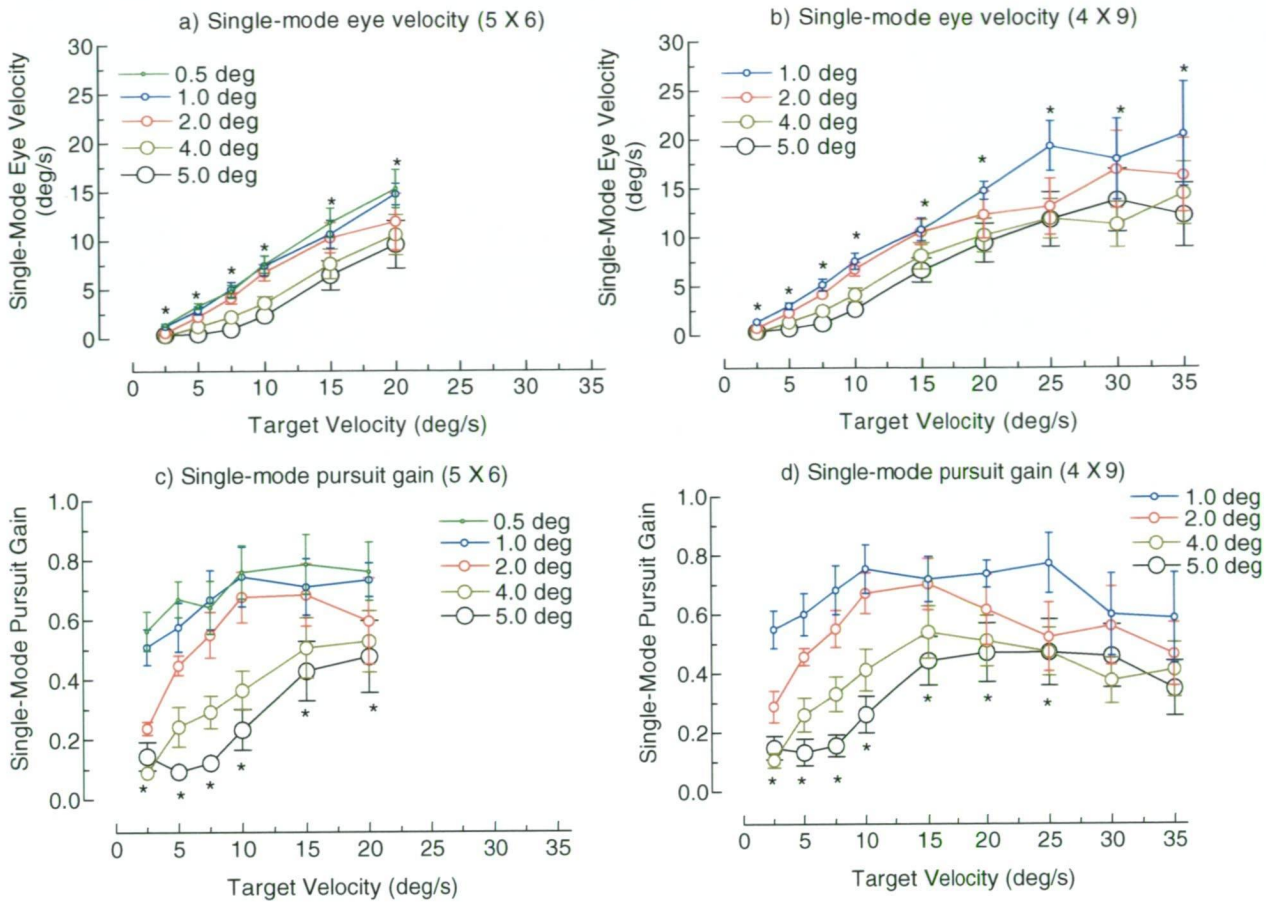

Figure 35. Interaction of spatial separation and target velocity on single-mode pursuit eye velocity (a and b) and gain (c and d) elicited by slashed motion stimuli (error bars depict *SE*; * denote significant effects of spatial separation, $p<.005$, significant spatial steps from 4.0 to 5.0 deg spatial separation).

Saccade frequency and characteristics as a function of spatial separation

Spatial separation did not affect saccade frequency per second or per cycle (see Table 7) when tracking slashed motion stimuli, but the characteristics of the saccades did change depending on spatial separation. As illustrated in Figure 36, increasing the spatial separation between targets was associated with larger and faster saccades of longer durations.

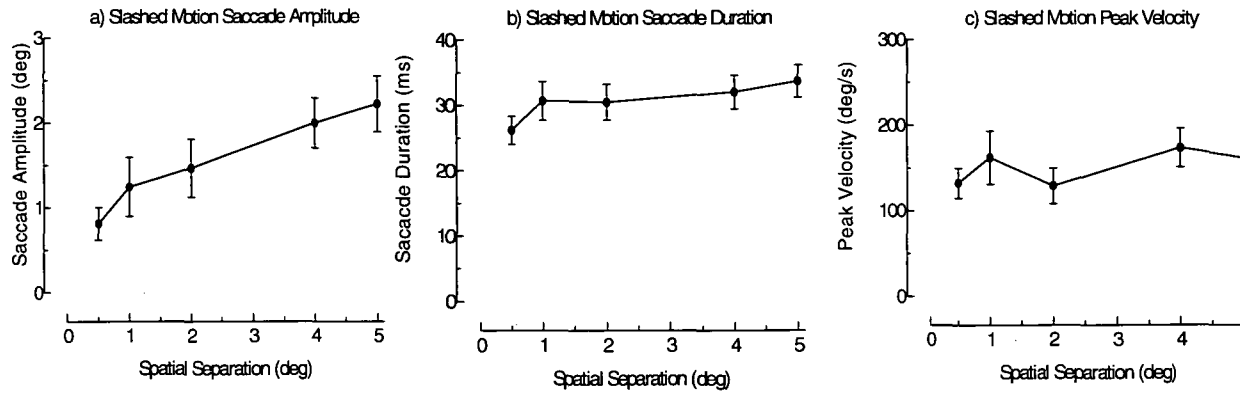

Figure 36. Main effect of spatial separation on (a) saccade amplitude, (b) saccade duration and (c) saccade peak velocity (error bars depict *SE*).

Ratio of saccadic versus smooth pursuit eye movements as a function of spatial separation

Increases in spatial separation did not affect the time-based saccade ratio measure (see Table 7), but the ratio of spatial distance covered by saccades versus pursuit eye movements increased significantly and linearly [$F(1,4)=29.7, p<.01, \eta^2=.88$] with increasing spatial separation, as shown in Figure 37.

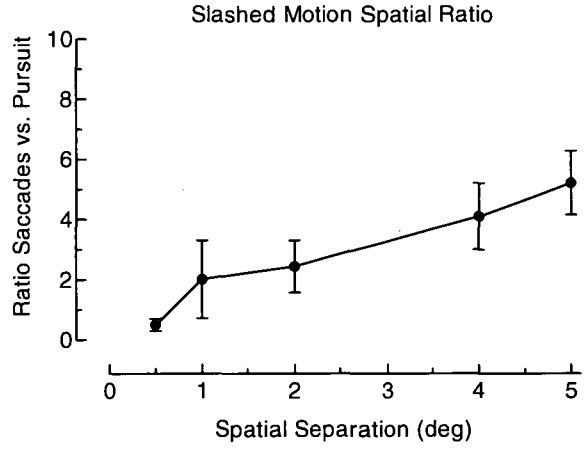

Figure 37. Distance-based ratio of saccadic versus smooth pursuit eye movements in the tracking of slashed motion (error bars depict *SE*).

A direct comparison of visual tracking of jumping-dot and slashed apparent motion

The initial analyses relating to stimulus duration that were presented in Table 3, revealed a significant interaction between the type of apparent motion and stimulus duration, and direct comparisons of visual tracking of jumping-dot and slashed motion therefore need to include stimulus duration as a factor. Results from the initial sets of five Type of Apparent Motion X Stimulus Duration X Spatial Separation X Target Velocity ANOVAs that relate to differences between jumping-dot and slashed motion are presented in this section and are summarised in Table 8. Results from these analyses relating to Stimulus Duration were previously reported in Table 3 (p.157), and the rationale for conducting these analyses were detailed on page 156. There were no significant three-or four-way interactions in any of these analyses and the detailed statistical output files are provided in Appendices E and F.

Table 8. Effects relating to the comparison of visual tracking of jumping-dot and slashed motion stimuli

Measure	Spatial Sep. (deg)	Target Velocity (deg/s)	Main Effect of Type of Apparent Motion	Type of Motion X Stimulus Duration	Type of Motion X Target Velocity
Dual-Mode Tracking					
Dual-Mode Eye Velocity	0.5,1,2,4,5	2.5	$F(1,5)=0.4,\eta^2=.08$	$F(2,8)=2.0,\eta^2=.29$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=2.4,\eta^2=.32$	$F(2,10)=1.4,\eta^2=.21$	$F(1,6)=1.9,\eta^2=.28$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=2.5,\eta^2=.33$	$F(2,8)=1.3,\eta^2=.21$	$F(1,5)=1.9,\eta^2=.27$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=1.0,\eta^2=.17$	$F(1,7)=1.0,\eta^2=.17$	$F(1,7)=0.7,\eta^2=.12$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=0.8,\eta^2=.13$	$F(1,6)=1.8,\eta^2=.27$	$F(2,11)=1.1,\eta^2=.18$
Dual-Mode Gain	0.5,1,2,4,5	2.5	$F(1,5)=0.4,\eta^2=.08$	$F(2,8)=2.0,\eta^2=.29$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=1.5,\eta^2=.23$	$F(2,10)=1.7,\eta^2=.25$	$F(1,6)=0.1,\eta^2=.01$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=2.1,\eta^2=.29$	$F(2,9)=1.4,\eta^2=.22$	$F(2,8)=0.6,\eta^2=.11$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=1.7,\eta^2=.25$	$F(2,8)=1.4,\eta^2=.21$	$F(3,13)=1.5,\eta^2=.24$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=1.7,\eta^2=.26$	$F(1,7)=2.0,\eta^2=.28$	$F(3,17)=2.3,\eta^2=.32$
Single-Mode Pursuit					
Single-Mode Eye Velocity	0.5,1,2,4,5	2.5	**$F(1,5)=23.8,\eta^2=.83$***	**$F(2,9)=14.7,\eta^2=.75$***	--
	1,2,4,5	2.5,5,7.5	**$F(1,5)=29.7,\eta^2=.86$***	**$F(1,7)=16.3,\eta^2=.77$***	**$F(1,6)=23.3,\eta^2=.82$***
	2,4,5	2.5,5,7.5,10,15	**$F(1,5)=24.8,\eta^2=.83$***	**$F(1,7)=12.3,\eta^2=.71$***	**$F(1,6)=18.7,\eta^2=.79$***
	4,5	2.5,5,7.5,10,15,20,25,30	**$F(1,5)=18.8,\eta^2=.79$***	$F(1,7)=5.3,\eta^2=.52$^	**$F(2,9)=9.4,\eta^2=.65$***
	5	2.5,5,7.5,10,15,20,25,30,35	**$F(1,5)=13.3,\eta^2=.73$***	$F(1,6)=6.6,\eta^2=.57$^	$F(2,8)=5.1,\eta^2=.51$^
Single-Mode Gain	0.5,1,2,4,5	2.5	**$F(1,5)=23.6,\eta^2=.83$***	**$F(2,9)=14.9,\eta^2=.75$***	--
	1,2,4,5	2.5,5,7.5	**$F(1,5)=30.7,\eta^2=.86$***	**$F(1,7)=18.0,\eta^2=.78$***	**$F(2,9)=8.7,\eta^2=.64$***
	2,4,5	2.5,5,7.5,10,15	**$F(1,5)=25.7,\eta^2=.84$***	**$F(1,7)=14.5,\eta^2=.74$***	$F(2,8)=7.1,\eta^2=.59$^
	4,5	2.5,5,7.5,10,15,20,25,30	**$F(1,5)=21.0,\eta^2=.81$***	**$F(1,7)=9.3,\eta^2=.65$***	$F(2,11)=5.0,\eta^2=.50$^
	5	2.5,5,7.5,10,15,20,25,30,35	**$F(1,5)=17.6,\eta^2=.78$***	$F(1,6)=9.4,\eta^2=.65$^	$F(2,12)=2.7,\eta^2=.35$
Saccades					
Saccade Frequency per second	0.5,1,2,4,5	2.5	$F(1,5)=0.1,\eta^2=.02$	$F(2,8)=0.3,\eta^2=.05$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=0.1,\eta^2=.02$	$F(2,9)=0.6,\eta^2=.11$	**$F(2,9)=12.3,\eta^2=.71$***
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=0.1,\eta^2=.02$	$F(2,8)=1.2,\eta^2=.20$	$F(2,8)=1.8,\eta^2=.26$
	4,5	2.5,5,7.5,10,15, 20,25,30	$F(1,5)=0.1,\eta^2=.00$	$F(2,10)=0.6,\eta^2=.11$	$F(2,11)=1.0,\eta^2=.17$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=0.5,\eta^2=.09$	$F(2,9)=0.4,\eta^2=.08$	$F(3,13)=2.0,\eta^2=.29$
Saccade Frequency per cycle	0.5,1,2,4,5	2.5	$F(1,5)=0.1,\eta^2=.02$	$F(2,8)=0.3,\eta^2=.05$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=0.0,\eta^2=.00$	$F(2,9)=0.6,\eta^2=.11$	$F(1,6)=2.6,\eta^2=.34$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=0.0,\eta^2=.01$	$F(2,9)=1.1,\eta^2=.18$	$F(1,6)=2.7,\eta^2=.35$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=0.1,\eta^2=.03$	$F(2,9)=0.4,\eta^2=.07$	$F(2,10)=3.2,\eta^2=.39$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=0.1,\eta^2=.01$	$F(2,9)=0.1,\eta^2=.01$	$F(2,8)=3.1,\eta^2=.38$
Saccade Amplitude	0.5,1,2,4,5	2.5	$F(1,5)=4.0,\eta^2=.44$	$F(1,7)=5.4,\eta^2=.52$^	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=6.4,\eta^2=.56$	$F(1,7)=9.0,\eta^2=.64$^	**$F(2,9)=8.0,\eta^2=.61$***
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=7.5,\eta^2=.60$^	$F(1,6)=8.4,\eta^2=.63$^	$F(1,6)=2.6,\eta^2=.34$
	4,5	2.5,5,7.5,10,15, 20,25,30	$F(1,5)=3.3,\eta^2=.40$	$F(1,6)=2.6,\eta^2=.35$	$F(2,8)=1.1,\eta^2=.18$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=7.8,\eta^2=.56$^	$F(2,11)=1.3,\eta^2=.18$	$F(2,14)=2.5,\eta^2=.29$
Saccade Duration	0.5,1,2,4,5	2.5	$F(1,5)=2.4,\eta^2=.32$	$F(2,8)=3.8,\eta^2=.43$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=2.2,\eta^2=.31$	$F(2,8)=5.5,\eta^2=.53$^	$F(2,8)=1.3,\eta^2=.20$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=1.5,\eta^2=.23$	$F(2,9)=5.1,\eta^2=.51$^	$F(1,7)=1.0,\eta^2=.16$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=0.2,\eta^2=.04$	$F(2,8)=1.9,\eta^2=.27$	$F(1,7)=2.9,\eta^2=.37$
	5	2.5,5,7.5,10,15, 20,25,30,35	$F(1,5)=0.0,\eta^2=.00$	$F(2,10)=0.4,\eta^2=.08$	$F(3,13)=3.5,\eta^2=.41$
Saccade Peak Velocity	0.5,1,2,4,5	2.5	$F(1,5)=1.6,\eta^2=.24$	$F(2,8)=3.0,\eta^2=.38$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=2.4,\eta^2=.33$	$F(1,7)=5.8,\eta^2=.54$^	$F(1,6)=2.3,\eta^2=.32$
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=3.5,\eta^2=.41$	$F(1,7)=7.3,\eta^2=.60$^	$F(2,8)=0.8,\eta^2=.14$
	4,5	2.5,5,7.5,10,15, 20,25,30	$F(1,5)=1.1,\eta^2=.17$	$F(1,6)=3.1,\eta^2=.38$	$F(2,9)=0.4,\eta^2=.07$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=0.5,\eta^2=.10$	$F(1,5)=2.2,\eta^2=.30$	$F(2,9)=0.4,\eta^2=.07$
Time-based Saccade Ratio	0.5,1,2,4,5	2.5	$F(1,5)=0.0,\eta^2=.00$	$F(1,6)=0.5,\eta^2=.09$	--
	1,2,4,5	2.5,5,7.5	$F(1,5)=1.2,\eta^2=.20$	$F(2,8)=0.8,\eta^2=.15$	**$F(2,8)=10.1,\eta^2=.67$***
	2,4,5	2.5,5,7.5,10,15	$F(1,5)=1.9,\eta^2=.28$	$F(1,7)=1.6,\eta^2=.25$	$F(1,7)=2.6,\eta^2=.34$
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=0.2,\eta^2=.04$	$F(2,10)=1.7,\eta^2=.25$	$F(1,7)=0.6,\eta^2=.11$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=0.4,\eta^2=.08$	$F(2,9)=1.2,\eta^2=.19$	$F(1,7)=0.7,\eta^2=.12$
Distance-based Saccade Ratio	0.5,1,2,4,5	2.5	$F(1,5)=12.0,\eta^2=.71$^	$F(1,6)=8.3,\eta^2=.63$^	--
	1,2,4,5	2.5,5,7.5	**$F(1,5)=17.8,\eta^2=.78$***	$F(1,5)=10.3,\eta^2=.67$^	**$F(2,10)=9.7,\eta^2=.66$***
	2,4,5	2.5,5,7.5,10,15	**$F(1,5)=13.6,\eta^2=.73$***	$F(2,8)=7.4,\eta^2=.60$^	$F(2,9)=5.0,\eta^2=.50$^
	4,5	2.5,5,7.5,10,15,20,25,30	$F(1,5)=9.5,\eta^2=.65$^	$F(2,8)=6.0,\eta^2=.55$^	$F(2,11)=3.4,\eta^2=.40$
	5	2.5,5,7.5,10,15,20,25,30,35	$F(1,5)=8.1,\eta^2=.62$^	$F(2,8)=3.1,\eta^2=.38$	$F(2,9)=2.3,\eta^2=.32$

Note. For each dependent variable a set of five ANOVAs were conducted, together covering the whole range of stimulus durations, spatial separations and target velocities. -- denote no interaction as Target Velocity only had one value. There were no other significant effects involving Type of Motion and no significant 3-or-4-way interactions. ^$.05>p>.01$, *$p<.01$; significant effects are in bold.

Dual-mode tracking of jumping-dot and slashed apparent motion

There were no differences in dual-mode tracking eye velocity or gain for jumping-dot and slashed motion, demonstrating that the two apparent motion stimuli are tracked equally well when saccadic and smooth pursuit eye movements are combined.

Single-mode pursuit of jumping-dot and slashed apparent motion

Single-mode pursuit eye velocity and gain were generally higher in response to slashed motion than for jumping-dot motion (Table 8), which suggests that under identical conditions the added motion signal available in slashed motion improves smooth pursuit eye movements. There was, however, a significant interaction between the type of apparent motion and target velocity for single-mode eye velocity and gain (although this did not reach significant for all analyses, see Table 8). Pairwise comparisons between jumping-dot and slashed motion were conducted at each target velocity, with values averaged for spatial separation and stimulus duration (see Figure 38), and these showed that single-mode pursuit eye velocity in response to slashed motion was faster than for jumping-dot only at moderate velocities (15.0-25.0 deg/s).

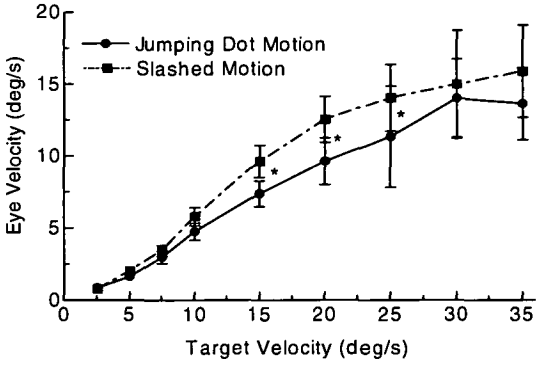

Figure 38. Interaction between the type of apparent motion and target velocity for single-mode pursuit eye velocity (* denote significant differences, p<.005; error bars depict *SE*).

The interaction between the type of apparent motion and target velocity was only significant for one of the analyses for single-mode pursuit gain and further analyses indicated that single-mode pursuit gain for the two types of motion did not differ significantly at 2.5 deg/s target velocity.

For single-mode pursuit eye velocity and gain there was also a significant interaction between the type of apparent motion and stimulus duration (Table 8). This was further analysed with pairwise comparisons (with Bonferroni-adjusted significance levels), with values averaged for spatial separation and target velocity (Figure 39), revealing some important findings. First, for slashed motion stimuli increasing the stimulus duration from 20 to 100ms did not affect single-mode eye velocity, but significantly improved single-mode pursuit gain. In contrast, for jumping-dot motion, increasing the stimulus duration from 20ms to both 60 and 100ms had a detrimental effect on both single-mode pursuit eye velocity and gain (see also Figure 42). Second, single-mode pursuit eye velocity and gain in response to slashed motion was only significantly superior to jumping-dot motion when stimulus duration exceeded 20ms.

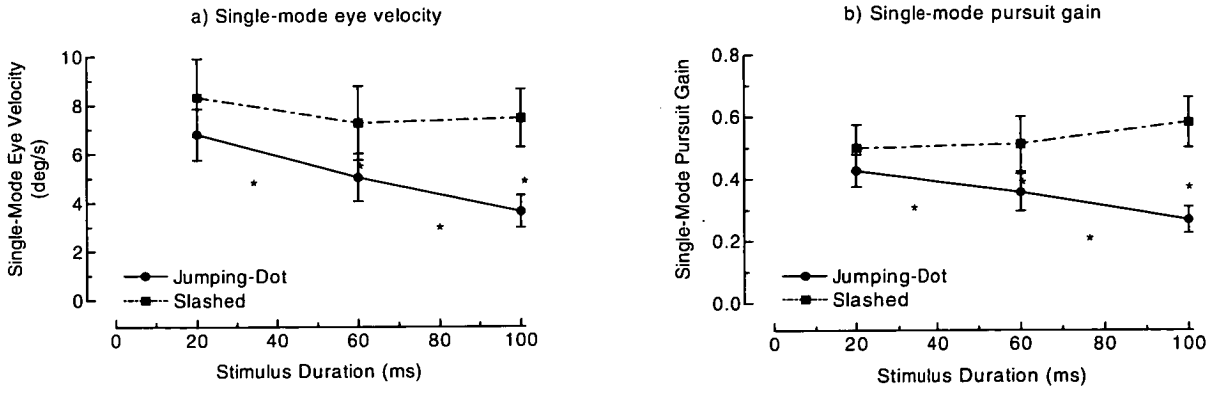

Figure 39. Interaction between type of apparent motion and stimulus duration for (a) single-mode pursuit eye velocity and (b) gain (* denote significant differences, $p<.007$; error bars depict *SE*).

To highlight the differences in single-mode pursuit gain in response to jumping-dot and slashed motion for the different stimulus durations, single-mode pursuit gain as a function of target velocity was graphed separately for each spatial separation and these are presented in Figure 40. At 20ms stimulus duration, peak performance for single-mode pursuit gain was at similar target speeds for jumping-dot and slashed motion: 10.0-15.0 deg/s for 0.5-2.0 deg spatial separation and 15.0-25.0 deg/s for 4.0 and 5.0 deg spatial separation. It is important to note that with increasing stimulus duration the peak for single-mode pursuit gain shifts to faster target velocities for jumping-dot motion, with peak pursuit gain for 60 and 100ms stimulus duration at faster target speeds (i.e., 20.0 deg/s for 2.0 deg spatial separation and 25.0-30.0 deg/s for 4.0 and 5.0 deg). In contrast, the peaks for single-mode pursuit gain for slashed motion shifts to slower target velocities with increasing stimulus duration, and peak pursuit gain for 60 and 100ms stimulus duration is at slower target speeds (i.e., 5-15 deg/s depending on spatial separation).

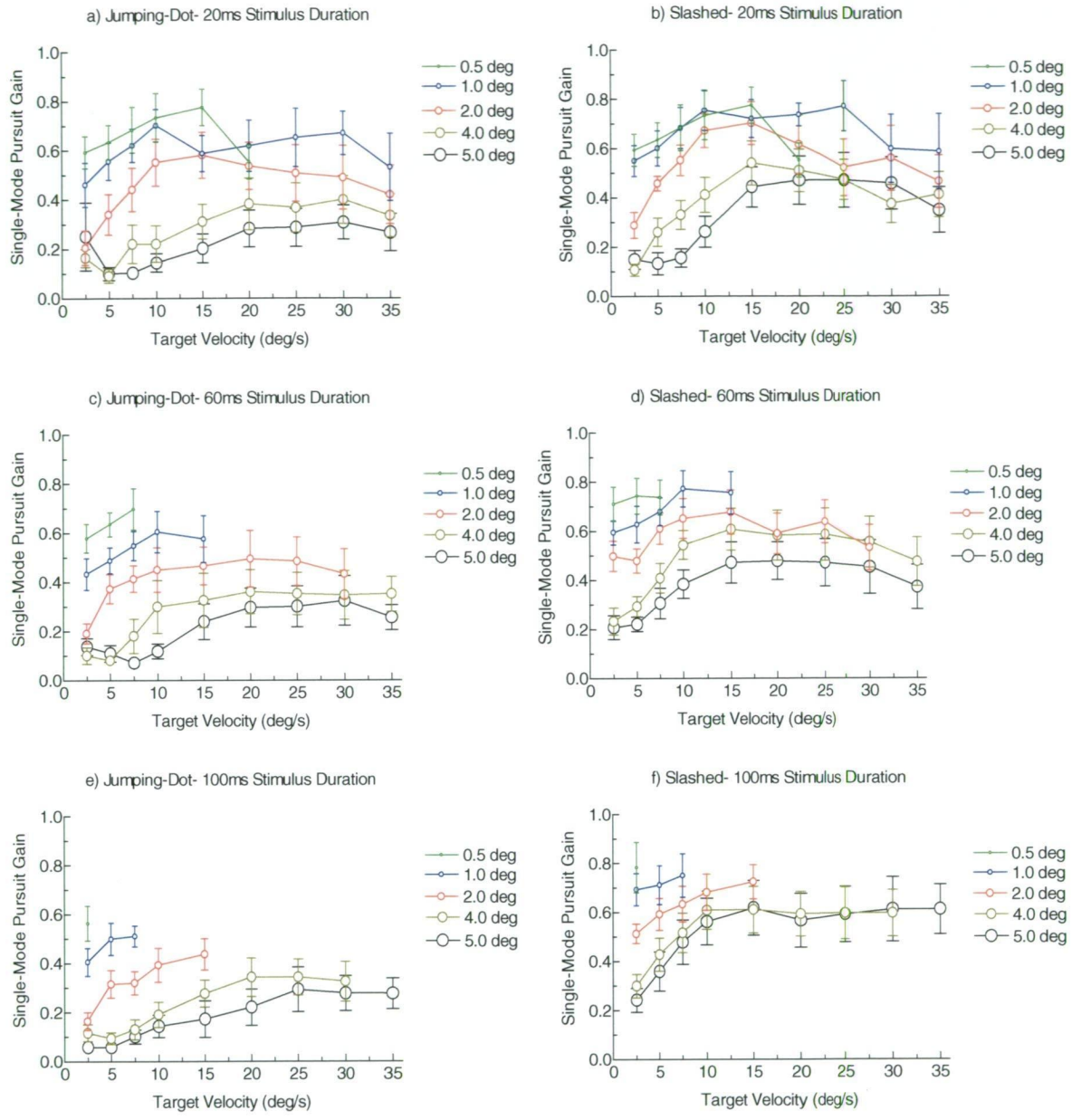

Figure 40. Functions of single-mode pursuit gain as a function of target velocity separately for each spatial separation in response to jumping-dot and slashed motion stimuli at 20ms (a & b), 60ms (c & d), and 100ms (e & f) stimulus duration. For jumping-dot motion, the peak pursuit gain shifts to faster velocities with increasing stimulus duration, and for slashed motion, peak pursuit gain shifts to slower target velocities. *Note*: For 60ms and 100ms stimulus duration not all target speeds are possible for all spatial separations.

Saccades elicited by jumping-dot and slashed motion stimuli

There were very few differences in the frequency or characteristics of saccades when tracking jumping-dot or slashed motion (Table 8). There were significant interactions between the type of apparent motion and target velocity for some saccade variables, including saccade frequency per second, saccade amplitude, and the distance-based and time-based ratio of saccadic versus pursuit eye movements. Follow-up analyses using pairwise comparisons suggested that the tendency for more frequent and larger saccades for jumping-dot than slashed motion was only significant for target velocities of 5.0-7.5 deg/s.

In addition, the distance-based ratio of saccadic versus pursuit eye movements was significantly larger when tracking jumping-dot than slashed motion stimuli, and there was also a significant interaction between the type of motion and spatial separation for the distance-based ratio measure. Pairwise comparisons showed that the tendency for a larger ratio of saccadic eye movements in the visual tracking of jumping-dot than slashed motion was only significant when spatial separations were large (i.e., 4.0 and 5.0 deg), as illustrated in Figure 41.

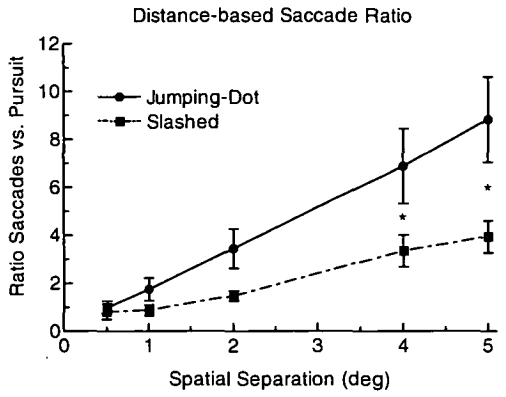

Figure 41. Ratio of spatial distance covered by saccades versus pursuit eye movements for jumping-dot and slashed motion for each spatial separation (* denote significant differences, $p<.01$; error bars depict *SE*). Note: These results are not included in Table 8, F-tests for the four analyses are: $F(2,10)=5.3$, $\eta^2=.51$^; $F(2,10)=13.7,\eta^2=.73$*; $F(2,9)=19.6,\eta^2=.80$*; $F(1,5)=6.8,\eta^2=.58$^.

Figure 42 displays eye traces for one representative participant and illustrates the differences in the visual tracking of jumping-dot and slashed motion that have been described thus far. Visual tracking of slashed motion becomes significantly smoother when stimulus duration increases, and the opposite effect is evident for jumping-dot motion. In addition, the eye traces again highlight that, for both types of apparent motion, visual tracking becomes smoother with a smaller number of larger, faster, and temporally longer saccades at faster target velocity.

Figure 42 also displays the eye velocity trace, which spikes whenever the eye accelerates quickly, such as when a saccade is generated. These velocity traces were examined thoroughly for all participants, in particular comparing the velocity traces for jumping-dot and slashed motion at short and long stimulus durations. There were no differences between jumping-dot and slashed motion, and the velocity trace did not exhibit any visible pulsatile acceleration as was described by Barnes and Asselman (1992) for their longer target exposures (80ms) of slashed motion.

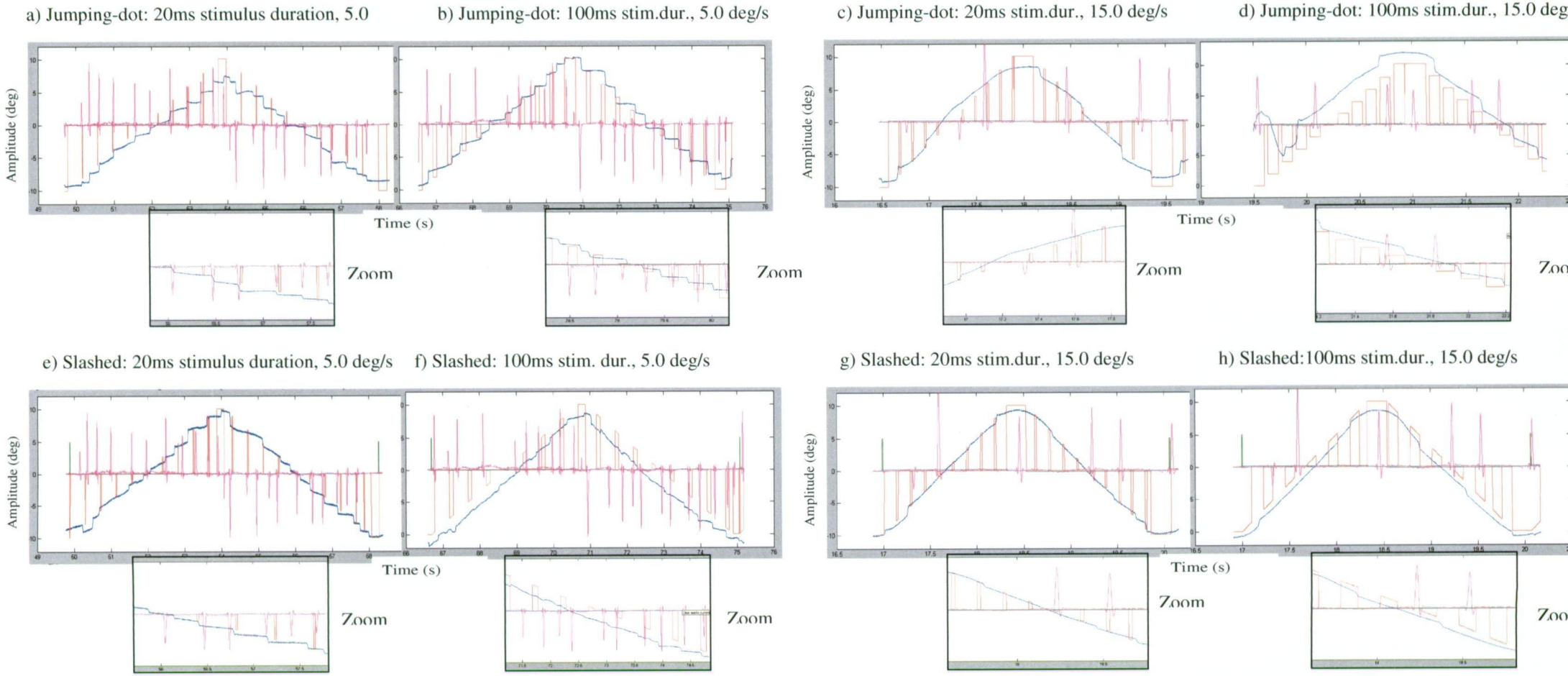

Figure 42. Eye traces (blue line) for a representative participant (DH) tracking jumping-dot and slashed motion at 2.0 deg spatial separation for 20ms and 100ms stimulus duration, at 5.0 and 15.0 deg/s target speed. For jumping-dot (a-d), increasing target exposure reduced single-mode pursuit gain, while for slashed motion (e-h) it increased single-mode pursuit gain. The pink line represents the velocity trace; the red trace represents the target stimulus.

Discussion

Summary of findings

1. Dual-mode tracking was equally accurate in response to continuous and apparent motion stimuli, and this was the case even at fast target velocities (up to 35.0 deg/s) and for large spatial separations (up to 5.0 deg).
2. Single-mode pursuit eye velocity and gain were superior in response to continuous than apparent motion stimuli, but only when spatial separation exceeded 2.0 deg for jumping-dot, and 4.0 deg for slashed motion.
3. For spatial separations of 2.0 deg or more there were more frequent saccades when tracking apparent compared to continuous motion stimuli, particularly at slow target velocity. There was also a tendency for larger saccades of longer duration in response to apparent motion and an overall greater ratio of spatial distance was covered by saccades compared to pursuit eye movements.
4. With increasing spatial separation for apparent motion stimuli single-mode pursuit eye velocity and gain decreased and the ratio of saccadic versus smooth pursuit eye movements increased, with larger saccades of longer duration at large spatial separations.
5. Single-mode pursuit gain for continuous motion decreased linearly with increasing target velocity, but single-mode pursuit gain elicited by apparent motion stimuli showed a quadratic trend as a function of target velocity, with lower pursuit gain at both slow and fast target speeds.
6. The optimal target velocity for peak single-mode pursuit gain depended on spatial separation, the type of apparent motion, and stimulus duration:

a. For both types of apparent motion, peak pursuit gain shifted to faster target velocities with increasing spatial separation.

b. For jumping-dot motion stimuli, peak single-mode pursuit gain shifted to faster target speeds when stimulus duration increased, while for slashed-motion stimuli, peak pursuit gain shifted to slower target speeds for longer stimulus durations.

7. At slow target velocities, a larger number of smaller, slower and briefer saccades were generated to cover the spatial trajectory, and in contrast, at fast target velocities, a small number of larger and faster saccades of longer duration were produced, but the distance-based ratio of saccadic versus pursuit eye movements was similar at slow and fast target speeds.
8. Single-mode pursuit velocity and gain of slashed motion could tolerate larger spatial separations (4.0 deg) than jumping-dot (2.0 deg) before being significantly lower than continuous motion. There was a larger ratio of saccadic versus pursuit eye movements when tracking jumping-dot than slashed motion with large spatial separations.
9. Single-mode pursuit eye velocity and gain were superior in response to slashed than jumping-dot motion, but only when stimulus duration exceeded 20ms. Single-mode pursuit eye velocity and gain improved when stimulus duration was increased for slashed, but deteriorated for jumping-dot motion.

Dual-Mode tracking is equivalent for continuous and apparent motion stimuli

Dual-mode tracking, which combines smooth pursuit and saccadic eye movements, was not affected by the type of motion stimulus, and dual-mode eye velocity and gain in response to jumping-dot and slashed apparent motion was equally as accurate as

for continuous motion stimuli. Dual-mode tracking eye velocity and gain in response to apparent motion were not affected by spatial separation, which means that even for apparent motion stimuli with targets spaced at intervals of up to 5.0 deg, visual tracking was as accurate as for a continuously moving target when saccadic and smooth pursuit eye movements are combined. Finally, dual-mode tracking gain was not affected by target speed and targets moving at velocities as fast as 35.0 deg/s were tracked with equal accuracy as targets moving at target speeds as slow as 2.5 deg/s. These findings demonstrate that when saccadic and smooth pursuit eye movements work in synergy, they can track even highly degraded and fast moving stimuli illustrating the high level of adaptability of human visual tracking, with eye movements able to adapt to a wide range of stimuli. It is important to note, however, that this accurate dual-mode tracking response is accomplished with significantly different combinations of saccadic and smooth pursuit eye movements, as evidenced by the fact that the type of motion stimuli, spatial separation and target velocity significantly affected saccadic and single-mode pursuit measures. This also confirms the importance of separating saccadic and smooth pursuit components of visual tracking as first proposed by Bahill, Iandolo, and Troost (1980).

Single-mode pursuit is superior in response to continuous than apparent motion stimuli for large spatial separations

For small spatial separations, there was no difference in single-mode pursuit eye velocity or gain in response to continuous and apparent motion stimuli, but smooth pursuit eye movements elicited by apparent motion deteriorated with increasing spatial separation. When spatial separations reached 2.0 deg for jumping-dot and 4.0

deg for slashed motion single-mode pursuit was significantly lower when tracking the apparent than continuous motion stimuli.

The fact that single-mode pursuit eye movements were elicited by apparent motion stimuli, and that these smooth pursuit eye movements were not distingushable from those in response to continuous motion stimuli up to a substantial spatial separation (2.0 and 4.0 deg, depending on the type of apparent motion), demonstrates that smooth pursuit eye movements can respond well to apparent motion stimuli, even when little or no actual retinal target velocity signal is available. Although this has previously been shown (e.g., Barnes & Asselman, 1992; M. M. Churchland & Lisberger, 2000; Morgan & Turnbull, 1978; Slaghuis et al., 2007a; Stone et al., 2000) this is the first study to demonstrate this systematically in maintained pursuit for a wide range of target velocities and spatial separations in human observers. Fetter and Buettner (1990) pointed out that such similarities between smooth pursuit of continuous and apparent motion can be explained because "even direction-selective neurons in the retina ... respond similarly to continuous motion or to sequentially flashed stimuli spaced over certain distances" (p.390), and they concluded that continuous and apparent mtoion stimuli create similar neural signals in the visual system. Energy models of visual motion perception also provide an explanation for similarities between continuous and apparent motion stimuli, because continuous and sampled stimuli share much spatio-temporal energy (Adelson & Bergen, 1985). Furthermore, these similarities in the smooth pursuit of continuous and apparent motion for small spatial separations are conistent with the notion that position information only, through image displacement, can be an adequate stimulus for pursuit (Behrens & Grüsser, 1979; Bridgeman, 1989; Heywood & Churcher, 1971;

Pola & Wyatt, 1980; Wyatt & Pola, 1981). It also suggests that perceived motion could be driving smooth pursuit (Beutter & Stone, 2000; Pola & Wyatt, 1980; Stone et al., 2000; Wyatt & Pola, 1979), because the computation of required eye velocity for jumping-dot motion stimuli relies on perceived target velocity based on target displacement.

The finding that for larger spatial separations in apparent motion single-mode pursuit eye velocity and gain was significantly better in response to continuous than apparent motion stimuli shows that when the apparent motion stimulus is sufficiently degraded it results in a smooth pursuit deficit. Churchland and Lisberger (2000) investigated jumping-dot motion in monkeys and they proposed that the initiation and maintenance phases of smooth pursuit are differentially affected by the degraded target stimulus in apparent motion, because these disruptions occurred at different parameters in their study. Their research focused on pursuit initiation and they proposed that the decreased performance in pursuit initiation for jumping dot motion stimuli was due to visuo-motor motion processing problems. Churchland and Lisberger (2000) also investigated the effects of temporal separation and target velocity on maintained pursuit and found significant pursuit deficits, particularly at fast target speeds, and they explained that during the maintenance phase poor pursuit is caused by a failure of the apparent motion stimulus to fully engage the pursuit system, which in turn results in eye velocity memory deficits. Applied to the results of the present research, this would suggest that the decreased single-mode pursuit performance for jumping-dot and slashed motion stimuli at large spatial separations is due to failure of eye velocity memory, because jumping-dot and slashed motion

stimuli exceeding spatial separation of 2.0 and 4.0 deg respectively cannot fully engage the pursuit system.

The idea that superior single-mode pursuit performance in response to continuous compared to apparent motion stimuli at large spatial separations is due to a failure of these highly degraded stimuli to fully engage the pursuit system receives support from the motion perception literature. As outlined in Chapter 5, there is a growing body of evidence suggesting that smooth pursuit eye movements and motion perception have shared underlying mechanisms and inputs. Research in visual perception has shown that the perception of motion involves motion detectors tuned to different spatial and temporal frequencies, and possibly different velocities (see Chapter 5). The detection of motion involves the integration of information from such receptors across space and time (Bours, Stuur, & Lankheet, 2007), and targets moving either slower or faster than the tuning characteristics of the motion detectors for particular velocities will show reduced or absent motion sensitivity to those velocities (see Ganz, 1975). Furthermore, while the visual system can sample continuous motion at any particular point in time of the target's trajectory, the perception of apparent motion relies on, and is limited to, the sampling of discrete visual events that need to meet certain spatio-temporal criteria to allow for sufficient sampling points to support the perception of motion. In other words, the perception of apparent motion is based more strongly on spatio-temporal integration, and how 'continuous' the perception of apparent motion is depends primarily on spatio-temporal factors, such as temporal separation, spatial separation and stimulus intensity (Korte, 1915; Neuhaus, 1930; Wertheimer, 1912). It then follows that when a motion stimulus is sufficiently degraded so that it is no longer perceived as continuous motion, it will

also no longer support smooth pursuit eye movements to the same degree. This explanation for decreased smooth-pursuit performance for highly degraded apparent motion stimuli implies a strong overlap of mechanisms underlying motion perception and pursuit, which is supported by the available evidence for shared inputs to motion perception and pursuit (see Chapter 5), as well as more specific evidence of general agreements between the spatio-temporal parameters supporting motion perception and smooth pursuit (M. M. Churchland & Lisberger, 2000). In order to further investigate this explanation a direct comparison of motion perception and smooth-pursuit eye movements of continuous and apparent motion would be required.

Saccade frequency, characteristics and ratio are of greater magnitude when tracking apparent than continuous motion stimuli

The main sequence relationships for saccades produced in the tracking of both jumping-dot and slashed motion follow the main sequence relationship that have been described for saccades to both stationary and continuously moving targets (e.g., De Brouwer, Missal et al., 2002). The similiarity in the main sequence relationship of saccades generated in the visual tracking of apparent motion stimuli and saccades produced for stationary and continuously moving targets strongly suggests that they are generated by similar mechanisms, as has been previously suggested (Kimmig et al., 2002), even though saccades to moving targets also consider velocity signals in their programming (e.g., Gellman & Carl, 1991; Keller & Johnsen, 1990).

When spatial separation for the apparent motion stimuli exceeds 2.0 deg a greater number of saccades per second and per cycle were generated in the tracking of apparent motion in comparison to continuous motion. There was also a tendency for

larger saccades of longer duration to be generated when tracking apparent motion stimuli with large spatial separations, and for a larger ratio of spatial distance to be covered by saccadic than smooth pursuit eye movements, but these effects did not consistently reach statistical significance. When the apparent motion stimuli were increasingly degraded due to larger spatial separations, differences in saccade variables between continuous and apparent motion stimuli increased.

Single-mode pursuit performance decreases and the contribution of sacacadic eye movements increases as a function of spatial separation for apparent motion stimuli

Single-mode pursuit eye velocity and gain in response to both jumping-dot and slashed apparent motion deteriorated with increasing spatial separation. This finding is consistent with findings for the effects of temporal separations in humans for jumping-dot (Morgan & Turnbull, 1978) and slashed motion (Barnes & Asselman, 1992), as well as findings for jumping-dot stimuli in monkeys for both temporal and spatial separation in single-mode pursuit initiation and temporal separation in smooth pursuit maintenance (M. M. Churchland & Lisberger, 2000). In the current study, single-mode pursuit was significantly disrupted when jumping-dot targets were spaced at 2.0 deg and more, with the most significant deteriorations in single-mode pursuit occurring with increases in spatial separation from 1.0-2.0 and from 2.0-4.0 deg. Single-mode pursuit of slashed motion could withstand larger spatial separation, but deteriorated for spatial separations of 4.0 deg and more, with the most significant deterioration occurring from 4.0 to 5.0 deg. This highlights that the smooth pursuit system can pursue even highly degraded jumping-dot and slashed apparent motion stimuli, because despite target separation of up to 2.0 and 4.0 deg (respectively), the

pursuit system was as well engaged as for continuous motion. Despite the decrease in single-mode eye velocity and gain, some smooth pursuit was still produced even at large spatial separations. This is consistent with the results of Barnes and Asselman (1992) who found that apparent motion stimuli with temporal separations as large as 960-1,000ms elicited single-mode pursuit eye movements. The current study investigated spatial rather than temporal separations but an examination of the functions of single-mode pursuit gain shows that when single-mode gain was highest for each apparent motion stimulus, temporal separation was generally in the range of 13-180ms. Barnes and Asselman (1992) proposed that for slashed motion, velocity may build up to high levels over the course of regular target presentations because of temporal summation of the transient responses, particularly for temporal separations below 1,000ms, and this allows relatively smooth tracking of the apparent motion stimulus. They also demonstrated that eye velocity is modulated in a pulsatile manner, especially when temporal separation exceeds 1,000ms, with eye velocity increasing with each target presentation and then decreasing exponentially during the subsequent target disappearance, consistent with research on transient target disappearance during maintained pursuit (e.g., Becker & Fuchs, 1985; Madelain & Krauzlis, 2003). In contrast, in the present study thorough examination of the visual traces did not reveal any differences between smooth pursuit of jumping-dot and slashed motion with regard to their velocity trace, and even at 100ms stimulus duration there was no visible pulsatile modulation of target velocity for slashed motion. This suggests that the summation of transient responses of each target presentation proposed by Barnes and Asselman (1992) occurred for all both types of apparent motion in the present study, which may be because only very few conditions in the present study had temporal separations exceeding 1,000ms (only when spatial

separations were 4.0-5.0 deg and target velocity was 2.5-5.0 deg/s). It is possible that longer temporal separations are required to evoke the pulsatile velocity trace depending on the stimulus characteristics. Alternatively, it is possible that the lack of pulsativel velocity trace in response to slashed motion in the current study reflects differences in the visual stimulus (e.g., the size of the stimulus in the current study was 15 min of arc, compared with 50 min of arc in Barnes & Asselman, 1992). In addition to the summation of the transient responses, Barnes and Asselman proposed that prediction effects over multiple presentations may enhance smooth pursuit of slashed motion because in their study eye velocity increased 200-300ms prior to each target appearance. Such prediction effects would have also contributed to the maintenance of eye velocity during the spatial gaps between targets for the two types of apparent motion in the present study.

Spatial separation of the apparent motion stimuli also had a significant effect on the saccades generated in visual tracking, with a significant increase of saccadic contribution to dual-mode tracking at larger spatial separations. With increasing spatial separation saccades were increasingly larger and of longer duration for both types of apparent motion, but saccade peak velocity only increased with increasing spatial separation for slashed motion stimuli. The ratio of the spatial trajectory covered by saccadic versus smooth pursuit eye movements also increased as a function of spatial separation. As discussed in Experiment 1, the distance-based ratio is the more valid measure of the saccadic component of dual-mode tracking, and it is also more consistent with other measures of saccadic and smooth pursuit eye movements. For example, the increase in the distance-based ratio of saccades versus pursuit eye movements as a function of spatial separation was consistent with a

parallel decrease in single-mode pursuit gain and parallel increases in the amplitude and duration of saccades. As discussed in Chapter 6, the time-based saccade ratio measure (Avila et al., 2003; Avila, Weiler et al., 2002) is often inconsistent with measures of saccade frequency and saccade characteristics because it is affected by temporal variables and the dynamics of the two types of eye movements. The spatial ratio on the other hand (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, L.E. Adler et al., 1999; R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999), which reports the spatial trajectory covered by saccadic versus pursuit eye movements, is more consistent with other measures. However, the spatial ratio data exhibits much greater variability than all other variables, resulting in decreased power for the statistical analyses, and it is therefore recommended that larger sample sizes are used when investigating this measure.

In conclusion, the findings relating to single-mode pursuit and saccadic measures indicate that when apparent motion stimuli are increasingly degraded, by increasing the spatial separation between targets, the performance of smooth-pursuit eye movements deteriorates. In parallel, the contribution of saccadic eye movements to dual-mode tracking increases through generating larger and temporally longer saccades (and faster saccades in the case of slashed motion) covering an increasingly larger proportion of the spatial trajectory.

Single-mode pursuit gain has different functional patterns in response to continuous and apparent motion stimuli as a function of target velocity

Single-mode pursuit velocity and gain were significantly affected by target velocity, but a very important finding of the present study is that single-mode pursuit gain for

continuous and apparent motion stimuli exhibited strikingly different functional patterns as a function of target velocity. More specifically, single-mode pursuit gain to continuous motion decreased linearly with increasing velocity, consistent with the findings of Experiment 1 at a similar range of target speeds. In contrast, single-mode pursuit in response to both jumping-dot and slashed motion stimuli followed a quadratic pattern as a function of target velocity, with lower single-mode pursuit gain at both slow and fast target velocities. In addition, differences in single-mode pursuit gain of continuous and apparent motion stimuli were much larger at slower target velocities. These findings were not expected and have not been described in the literature, and the most likely reason for this is that visual tracking of apparent motion stimuli have not previously been systematically investigated and compared with continuous motion over a large range of target speeds. Using jumping-dot stimuli in monkeys, Churchland and Lisberger (2000) found that single-mode pursuit deficits in response to apparent motion stimuli were more pronounced at fast target velocities, regardless of spatio-temporal parameters. The current study also found that single-mode pursuit eye velocity was significantly worse than for continuous motion at fast target velocities, but when comparing single-mode pursuit gain for continuous and apparent motion, it is evident that the deficits associated with apparent motion are actually more pronounced at slow target velocities (slower than 10.0-20.0 deg/s target velocity depending on spatial separation). The differences between the present findings and those reported by Churchland and Lisberger (2000) may reflect differences between the measures of eye velocity and gain, because their study only reported single-mode eye velocity to estimate pursuit performance. It is important to note that eye velocity is an absolute measure of smooth pursuit, which does not directly reflect how accurate pursuit performance is. Slaghuis, Hawkes, Holthouse,

and Bruno (2007a) also investigated jumping-dot, using a large range of target velocities, but as their study focused on comparing visual tracking in observers with schizophrenia and controls, they did not report direct statistical comparisons of single-mode pursuit eye movements for continuous and jumping-dot motion. The current findings on single-mode pursuit eye velocity are consistent with their results and show that deficits in single-mode pursuit eye velocity are more pronounced at fast target speeds, but the single-mode pursuit gain measure in the current study provides a more complete representation of the differences. While smooth pursuit of continuous motion deteriorated linearly with increasing target speed, single-mode pursuit gain in response to apparent motion followed a quadratic function, with decreased pursuit gain at both slow and fast target velocities, and the differences between single-mode pursuit gain of continuous and apparent motion stimuli are therefore much larger at slow target speeds.

The previous literature on smooth pursuit eye movements for continuous motion implies that smooth pursuit eye movements declines linearly as a function of target velocity. In contrast, the current data suggests that single-mode pursuit performance, similar to perceptual processes such as visual motion perception (Ganz, 1975), actually follows an inverted U-shape pattern resembling a band-pass function, with peak performance at a specific target velocity. In the case of motion perception, such a function reflects a trade-off between spatio-temporal characteristics of the stimulus such as target velocity and stimulus size or spatial frequency. The current findings clearly demonstrate such an inverted U-shape function for single-mode pursuit gain of apparent motion with increasing stimulus velocity, with lower single-mode pursuit gain at slow and fast target speeds. A similar lower velocity limit for smooth pursuit

of continuous motion has not yet been fully explored, but the little available evidence suggests that at slow target speeds the single-mode pursuit gain for continuous motion may indeed deteriorate (Carl & Gellman, 1987; M. M. Churchland & Lisberger, 2000; Spering et al., 2005). The findings of Experiment 1 and the present study indicate that if there is a lower velocity limit in response to continuous motion stimuli, it is below 2.5 deg/s velocity for a small single-dot target stimulus, because it was not evident for pursuit of continuous motion at the examined target speeds. Further investigations of a lower velocity limit for smooth pursuit eye movements elicited by continuous motion stimuli therefore need to include target speeds below 2.5 deg/s.

Peak single-mode pursuit gain depends on spatial separation, type of apparent motion, and stimulus duration

The optimal target velocity resulting in the peaks on the quadratic functions for single-mode pursuit gain depends on the type of apparent motion, spatial separation, and stimulus duration. A similar shift in peaks have been reported in visual motion perception with optimal velocity for peak motion sensitivity depending on other variables, such as the stimulus size (Bonnet, 1980) or the spatial frequency of the target (Burr & Ross, 1982; Watanabe et al., 1968). The current findings showed that optimal stimulus velocity for peak single-mode pursuit gain was at higher velocities for larger spatial separations and this was the case for both jumping-dot and slashed motion stimuli. At 20ms stimulus duration, peak single-mode pursuit gain was at target velocities of 10.0-15.0 deg/s when spatial separation was small (0.5-2.0 deg), but when spatial separation was 4.0 and 5.0 deg, highest pursuit gain was at 20.0-30.0 deg/s target speed. The optimal target velocity for peak single-mode pursuit gain also

depended on stimulus duration, but this effect was different for the two types of apparent motion stimuli. At 20ms stimulus duration, peak single-mode pursuit gain was reached at similar target velocities for both types of apparent motion stimuli (depending on spatial separation), but for longer stimulus durations (60 and 100ms), peak single-mode pursuit gain shifted to faster target velocities for jumping-dot and to slower target velocities for slashed motion stimuli.

The findings that optimal target velocities for peak single-mode pursuit gain depended on spatial separation, type of apparent motion, and stimulus duration demonstrate that single-mode pursuit of apparent motion stimuli depends on the spatio-temporal parameters of the apparent motion stimulus. Churchland and Lisberger (2000) reported that their findings in monkeys suggested that target speed affected single-mode pursuit regardless of spatio-temporal parameters of the stimulus. As previously mentioned, their study only reported pursuit eye velocity, and in the present study, single-mode pursuit *eye velocity* would also suggest a general deterioration of pursuit with increasing target speed. In contrast, the findings for single-mode pursuit *gain* in the present study shows that the effects of target velocity depend strongly on the spatio-temporal parameters of the target stimulus, and that target velocity has an indirect effect on single-mode pursuit of apparent motion because target velocity mediates the spatio-temporal parameters of the target stimulus to an 'optimal' combination. These findings in relation to single-mode pursuit gain are consistent with findings in visual perception, because the perception of motion also depends on the spatio-temporal parameters of the target stimulus. More specifically, the perception of motion is based on directionally selective motion detectors (see Chapter 5), which are constrained with regard to their spatial

distributions and inherent time delays (Snowden & Braddick, 1989a) and motion perception depends on the integration of spatial changes over time or spatio-temporal integration (Ganz, 1975; Sekuler et al., 1990). The perception of apparent motion is based on spatio-temporal integration, and how 'continuous' the perception of apparent motion is depends primarily on spatio-temporal factors, such as temporal separation, spatial separation, and stimulus intensity (Korte, 1915; Neuhaus, 1930; Wertheimer, 1912). If apparent motion meets adequate spatio-temporal criteria to facilitate spatio-temporal integration, motion is perceived, and it has been clearly demonstrated that for random-dot kinematograms the maximal spatial separation (d_{max}) supporting motion perception increases with multiple presentations over space and time (Snowden & Braddick, 1989a, 1989b). Furthermore, it has been shown that apparent motion can be perceived between stimuli that are spaced at distances that are too great for them to stimulate the same receptive fields (Smith, 1948). Visual motion perception is enhanced by increasing the target velocity when there is a large spatial distance between successive targets, because it decreases the temporal delay between the successive stimulation of spatially distant receptors, and increases the number of presentations within the same time period. Single-mode pursuit gain in the present study exhibited a similar pattern, and this provides strong, albeit indirect, evidence that smooth pursuit eye movements and motion perception have shared inputs. A direct comparison of single-mode pursuit gain with visual motion perception under the same experimental conditions would provide more direct evidence.

Mechanisms underlying the different functions of single-mode pursuit gain as a function of target velocity

There are two possible explanations for the differences in functions for single-mode pursuit gain of continuous and apparent motion stimuli with increasing target velocity. First, it is possible that single-mode pursuit eye movements in response to continuous and apparent motion stimuli have different functional patterns as a function of target velocity. This would mean that single-mode pursuit gain for continuous motion follows a function with a monotonic decline, as generally implied in the literature (see Chapter 2), while single-mode pursuit gain of apparent motion follows an inverted U-shape, or band-pass function, reflecting differences in mechanisms underlying smooth pursuit of these different motion stimuli. Single-mode pursuit for continuous motion is generally believed to be driven predominately by retinal velocity signals (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Eckmiller, 1987; Pola, 2002; Pola & Wyatt, 1991; Rashbass, 1961; D. A. Robinson, 1965; Young & Stark, 1963), whereas single-mode pursuit of jumping-dot and brief presentations of slashed motion are driven by retinal position and/or perceived motion, because there is a weak or no velocity signal (e.g., Krauzlis & Stone, 1999; Pola & Wyatt, 1980). Visual motion perception has been shown to follow a band-pass function and it is therefore possible that only the function for single-mode pursuit gain for apparent motion resembles a band-pass function, because it is driven by perceived motion, but that the pursuit gain for continuous motion declines linearly, because it is driven by stimulus-velocity. In a similar way, the visual perception of continuous and apparent motion were originally believed to be generated by different mechanisms (Anstis, 1978; M. Green & Von Grunau, 1983; Kolers, 1972, 1983), but

the fact that current evidence no longer supports this view (e.g., Anstis, 1986; Burr, 1991; Gregory & Harris, 1984; Larsen et al., 2006), suggests that smooth pursuit eye movements for continuous and apparent motion are also generated by similar mechanisms.

The more likely explanation for the different functions for pursuit gain of continuous and apparent motion stimuli found in the present study is that single-mode pursuit gain in response to both motion stimuli follow an inverted U-shape or band-pass function, but that the spatio-temporal parameters in the current study did not capture this for continuous motion. The current study showed that the peak for single-mode pursuit gain in response to jumping-dot stimuli shifts to faster target velocities with increasing stimulus duration, but to slower target velocities for slashed motion stimuli. Because continuous motion stimuli can be conceptualised as slashed motion with extended stimulus duration, it is likely that gain for continuous motion also follows a band-pass function, but with its peaks shifted to very low target speeds that are not covered in this study's range of target velocities. This would suggest that single-mode pursuit of continuous and apparent motion are generated by similar mechanisms, but with different preferred target velocities. These explanations can be tested by way of a direct comparison of single-mode pursuit of continuous and apparent motion stimuli using slower target velocities.

Explanations for the deterioration of single-mode pursuit gain at slow and fast target velocities for apparent motion stimuli

The quadratic function for single-mode pursuit gain of apparent motion stimuli as a function of target velocity shows a clear decrease in single-mode pursuit gain at both

slow and fast target velocities, with peak pursuit gain at moderate target speeds, depending on the spatio-temporal characteristics of the stimulus. The decrease in single-mode pursuit gain for apparent motion stimuli at *fast* target velocities is similar to that found for continuous motion stimuli (in the present study and Experiment 1), and it is therefore likely to be due to similar factors, which were discussed in Chapter 6. Once target velocity exceeds the optimal target speed for a given motion stimulus, eye velocity is slower than target velocity, and the eye starts lagging behind the target. The main difference between continuous and apparent motion is that for apparent motion stimuli, optimal target velocities are at fast target speeds. The decrease in single-mode pursuit gain for apparent motion stimuli at *slow* target velocities is most likely due to the pursuit system not getting fully engaged by the apparent motion stimuli moving at slow target speeds. Lamontagne (1973) proposed the existence of a lower velocity limit for single-mode pursuit of apparent motion, based on the idea that slow target speeds would not supply sufficient sample-points within a certain time period to initiate and maintain smooth pursuit eye movement. Hence, the spatio-temporal parameters of apparent motion at slow target velocities do not enagage pursuit, resulting in a failure of the visuo-motor drive to initiate and maintain smooth pursuit eye movements, as suggested by Churchland and Lisberger (2000) for pursuit initiation. Furthermore, the smooth pursuit system cannot utilise any prediction based on the estimate of periodicity, smooth-pursuit eye movements cannot benefit from this information to enhance pursuit gain, and therefore single-mode pursuit gain remains low at slow target speeds.

Saccade frequency, characteristics and ratio as a function of target velocity

Saccade frequency per second increased with increasing target velocity and in contrast, saccade frequency per cycle decreased as a function of velocity, consistent with the findings of Experiment 1. This shows that these differences between the two saccade frequency measures apply not only to continuous motion, but also to apparent motion stimuli, and as mentioned previously, this highlights the importance of choosing and specifying the measure of saccadic frequency. As discussed in Chapter 6, both measures of saccade frequency are affected by temporal variables such as the overall crossing time, and this also demonstrates the need for cautious interpretation of these measures at different target speeds, and the need to take into account the characteristics of the saccades in these interpretations.

In relation to the characterstics of saccades as a function of target speed, saccade duration, peak velocity, and amplitude (for jumping-dot, but not slashed motion stimuli) increased with increasing target velocity. In combination with the decrease in saccade frequency per cycle, these findings suggest that at slow target velocities, a small number of smaller, slower and briefer saccades are generated, and in contrast, at fast target speeds a smaller number of larger, faster, and temporally longer saccades are produced. Even though the dynamcis of saccadic eye movements are different at slow and fast target velocities, the overall distance-based ratio of saccadic versus pursuit eye movements generated to cover the spatial trajectory remains unchanged with increasing target velocity. The distance-based ratio even shows a significant quadratic function, mirroring that of single-mode pursuit gain for apparent motion stimuli, which demonstrates that the proportion of saccadic eye movements to cover

the motion trajectory increases when single-mode pursuit gain decreases. In addition, these findings demonstrate that the saccadic contribution to dual-mode tracking is not a one-dimensional mechanism that simply increases the number of saccades when the eye lags behind the target, but instead it appears to be a more dynamic process that complements single-mode pursuit in different ways at slow and fast target speeds. This also demonstrates that even though the distance-based saccadic ratio is a good measure to *quantify* the absolute saccadic contribution to dual-mode tracking, it should be interpreted in conjunction with saccade frequency per spatial unit and saccade characteristics in order to *qualify* the contribution of saccadic eye movements to dual-mode tracking.

The pattern of an increasing saccadic contribution when single-mode pursuit gain decreased and vice versa was consistently observed in the present study, and it is consistent with the notion that saccades are generally a consequence of single-mode pursuit deficits (M. M. Churchland & Lisberger, 2000), but not in the same way at slow and fast target speeds. At fast target velocities, saccades are triggered by position errors caused by the eye lagging behind the target when eye velocity no longer matches target velocity very well because the upper limit of smooth pursuit is reached, as has been suggested previously (see e.g., R. H. S. Carpenter, 1988). The results of the current study, however, show that not the frequency of saccades increase with increasing target velocity, but the magnitude of saccade characteristics. It is possible that this is partly due to the refractory period, which inhibits saccade generation for a period of time after the saccade is made (see Chapter 2). The position error accumulated in the same refractory period is significantly larger at fast target velocities, requiring larger saccades to catch up with the target. While this can explain

some of the current findings at faster target speeds, if this was the only factor we would expect a purely linear relationship between saccade frequency, saccade amplitude and target velocity. What we find instead is a more quadratic relationship with a large saccadic contribution at both slow and fast target speeds. At slow target velocities single-mode pursuit gain is low, most likely because the stimulus is not sufficient to engage smooth pursuit, and the target is therefore tracked predominately with saccadic eye movements, triggered by small position error caused by the discrete displacements of the target. The current study does not provide any direct evidence for a velocity input into saccadic eye movements, but the fact that at fast target speeds accurate saccades are produced despite the eye remaining in motion does suggest that velocity signals are incorporated into saccade programming, as has been previously proposed (Blohm et al., 2003; Gellman & Carl, 1991; Ron et al., 1989b).

Differences in single-mode pursuit and saccadic measures for jumping-dot and slashed motion stimuli

Jumping-dot and slashed apparent motion stimuli in the present study only differ in that jumping-dot motion stimuli only provide position information (through image displacement) and a perceived velocity signal has to be computed by the visual system, while slashed motion stimuli provide position information as well as a brief retinal velocity signal. The findings of Experiment 2 that have been described so far show very similar visual tracking for jumping-dot and slashed motion, but there are also some differences that need to be discussed. First, single-mode pursuit gain in response to jumping-dot motion was significantly worse than for continuous motion when spatial separations were 2.0 deg and more, but spatial separations of 4.0 deg and more were required for significant differences between slashed and continuous

motion. This is consistent with separate findings that single-mode pursuit for jumping dot motion is significantly affected for temporal separations exceeding 150ms for jumping-dot (Morgan & Turnbull, 1978), but exceeding 300ms for slashed motion (Barnes & Asselman, 1992). Motion is generally conceptualised as change in position over time (e.g., Sekuler et al., 1990) and there is evidence that position and velocity information are processed separately (Abrams & Landgraf, 1990; Smeets & Brenner, 1995). The finding that jumping-dot motion stimuli with small spatial separations can elicit single-mode pursuit that is not distinguishable from that for continuous motion demonstrates that position information can be processed in the absence of a velocity signal to produce an adequate motion signal to engage the smooth pursuit system, as previously proposed (Barnes et al., 1987; Behrens & Grüsser, 1979; Heywood & Churcher, 1971; Morgan & Turnbull, 1978; Pola & Wyatt, 1980; Wyatt & Pola, 1981). Nevertheless, the fact that slashed motion is disrupted at larger spatial separations than jumping-dot motion shows that the velocity signal in slashed motion directly affects the smooth pursuit system, enhancing smooth pursuit eye movements and making them more resistant to degradation by increasing spatial separation. Together these findings demonstrate that both position and velocity information can provide an input into the smooth pursuit eye movement system, with the available velocity signal being added to the position information. This is consistent with the view that position information or perceived motion can function to supplement retinal target motion to optimise smooth pursuit performance when the target motion signal is absent or weak (Pola & Wyatt, 1991), but that velocity signals provide the main input when available (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Eckmiller, 1987; Pola, 2002; Pola & Wyatt, 1991).

The second difference between jumping-dot and slashed motion was expected based on previous findings of the effects of target presentation on jumping-dot (Barnes et al., 1987) and slashed motion (Barnes & Asselman, 1992) individually: single-mode pursuit of the two apparent motion stimuli was differently affected by stimulus duration. Under identical experimental conditions, single-mode pursuit eye velocity and gain for slashed motion improved significantly when stimulus duration was increased from 20 to 100ms. In contrast, single-mode pursuit gain for jumping-dot stimuli significantly deteriorated with increasing stimulus duration from 20 to 60, and 100ms. Based Barnes, Donnelly, and Eason's (1987) and their own results, Barnes and Asselman (1992) concluded that for stimulus durations exceeding 30ms, the motion signal available to the visual system in slashed motion 'synergistically' increases single-mode pursuit eye velocity, while a stationary jumping-dot target 'antagonistically' slows eye velocity during target exposure (p.635). The current study, which directly compared the two apparent motion stimuli for identical stimulus parameters, provides the first direct evidence to support this idea. The synergistic effect of the velocity signal available during target exposure to the slashed motion stimulus accumulates over repeated target presentations because of temporal summation (Barnes & Asselman, 1992), which increases eye velocity, and the longer the duration of the velocity signal, the better the velocity signal available to the pursuit system. This accumulation of the velocity signal over repeated presentations in slashed motion explains why an increase in stimulus duration results in higher single-mode pursuit eye velocity and gain, and it also explains why slashed motion can withstand larger spatial separations than jumping-dot motion, because the jumping-dot stimulus does not provide such a retinal velocity signal. In addition, this helps to explain the previously reported effect that peak single-mode pursuit gain for

jumping-dot motion shifts to faster target velocities with increasing stimulus duration, but to lower target velocities for slashed motion. Because an increase in stimulus duration enhances eye velocity due to an accumulation of the velocity signal over repeated presentations, the spatial separation between targets can be overcome at slower target velocities. In contrast, the antagonistic effects of exposure to the stationary jumping-dot targets slow smooth pursuit eye movements, and faster target velocities are therefore required to overcome the separation of the targets to generate smooth eye movements.

Finally, differences in single-mode pursuit gain in response to jumping-dot and slashed motion stimuli were only significant once stimulus duration exceeded 20ms, and this is consistent with Barnes and Asselman's (1992) proposal that the velocity signal available in slashed motion can only be processed by the visual system when stimulus duration is 30ms or more. But even though direct comparisons of single-mode pursuit eye velocity and gain were only significant at stimulus durations exceeding 20ms, the differences in spatial separation required to significantly disrupt single-mode pursuit for jumping-dot and apparent motion were obtained at 20ms stimulus duration. This suggests that over multiple presentations of the slashed motion stimulus, some processing and accumulation of the velocity signal must occur even at 20ms stimulus duration. This is further supported by the fact that some differences between jumping-dot and slashed motion stimuli were also found for saccade variables at 20ms stimulus duration. This suggests that even though Barnes and colleagues considered 20ms to be too short to convey any velocity information (Barnes & Asselman, 1992; Barnes et al., 1987), some processing of the velocity signal must occur even at this short stimulus duration. In summary, there is evidence

that the velocity signal is not fully processed unless stimulus duration exceeds 20ms, but some processing of the velocity signal over multiple presentations occurs even at 20ms stimulus duration. Nevertheless, when the two tasks are compared directly, it is recommended that stimulus durations above 30ms be selected, to allow sufficient time for the velocity signal to be fully processed. This needs to be balanced with the fact that long stimulus durations (i.e. above 60ms) restrict the range of target velocities that can be tested and they also make pursuit of slashed motion more and more similar to continuous motion. These factors also need to be considered when selecting stimulus duration in the investigation of visual tracking of apparent motion stimuli.

The differences between jumping-dot and slashed motion revealed in the present study, which demonstrate that position and velocity input can be experimentally separated, have great potential for the study of visual tracking. For example, this paradigm could be used with observers with schizophrenia to further investigate whether they can make use of both position and velocity information in the same way as normal observers. More specifically, if single-mode pursuit gain in observers with schizophrenia is significantly better in response to slashed than jumping-dot motion, as is the case for normal observers, this would suggest that they can process the velocity signal available in slashed motion in a normal way and may exclude velocity processing as a cause for the visual tracking deficit in schizophrenia.

Summary and conclusions

The aim of Experiment 2 was to compare saccadic and smooth pursuit eye movements in the visual tracking of jumping-dot and slashed apparent motion stimuli

with that of a continuously moving target for a wide range of spatio-temporal parameters. The two particular areas of interest were the interplay between the two types of eye movements during tracking, and to identify the spatio-temporal conditions that favour one eye movements over the other. Dual-mode tracking performance, combining saccades and smooth pursuit, was equivalent for continuous motion and systematically degraded apparent motion stimuli, but this was accomplished with different combinations of saccadic and smooth pursuit eye movements, depending on the type and spatio-temporal parameters of the stimulus. Single-mode pursuit gain in response to a continuously moving target was highest at the slowest target speed (2.0 deg/s) and decreases linearly as a function of target velocity. In contrast, single-mode pursuit gain elicited by both apparent motion stimuli followed a quadratic function, with low gain at both slow and fast target velocities. The question remains whether these different functions for continuous and apparent stimuli reflect actual differences in the mechanisms underlying smooth pursuit of continuous and apparent motion, or whether the target speeds investigated in the present study were too fast to capture the quadratic function for single-mode pursuit gain of continuous motion.

The stimulus velocity at which single-mode pursuit gain in response to apparent motion reached its peak depended on the spatio-temproal parameters of the target stimulus. More specifically, for both apparent motion paradigms peak single-mode pursuit gain shifted to faster target velocities with increasing spatial separation. Also, while single-mode pursuit gain shifted to faster velocities with increasing stimulus duration for jumping-dot stimuli, it shifted to slower target velocities for slashed motion stimuli. These findings indicate that when the spatio-temporal parameters for

each type of apparent motion are at preferred levels for smooth pursuit eye movements, single-mode pursuit gain is at peak levels and the saccadic contribution to dual-mode tracking is smallest. When target velocities are below optimum, single-mode pursuit gain decreases because the apparent motion stimulus is not sufficient to fully engage the pursuit system, resulting in an increasingly larger number of saccadic eye movements, triggered by the position error produced by the discrete displacements of the apparently moving target. In contrast, when stimulus velocity increases beyond optimal velocity for smooth pursuit for a given stimulus, single-mode pursuit eye velocity no longer matches target velocity, resulting in the eye lagging behind the target and the position error caused by this lag triggers corrective saccades, resulting in a smaller number of saccades of greater amplitude, velocity, and duration. This demonstrates that the contribution of saccades is different at slow and fast target velocities, and that saccade generation during visual tracking is not the one-dimensional process of an increase in saccade frequency with increasing target velocity that has been suggested in the literature (e.g., Ciuffreda & Tannen, 1995; Hallett, 1986; Lisberger et al., 1987).

The quadratic functions found for single-mode pursuit gain as a function of target velocity, and the shift in peak gain depending on the spatio-temporal paremeters demonstrate that the spatio-temporal parameters of the apparent motion stimulus must meet adequate criteria for smooth pursuit eye movements to be generated. These criteria are similar to those previously reported for the perception of apparent motion, which provides support for the idea that motion perception and pursuit have shared inputs. Furthermore, the current findings demonstrate that position information (through image displacement) can be an adequate stimulus driving pursuit, because

jumping-dot motion stimuli with spatial separations below 2.0deg, elicited pursuit equal to that for continuous motion. Nevertheless, the additional velocity signal available in slashed motion enhances single-mode pursuit eye movements, lending support to the idea that when available, velocity signals provide the main input for smooth pursuit (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Eckmiller, 1987; Pola, 2002; Pola & Wyatt, 1991), but position signals can supplement visual processing for pursuit when the target motion signal is absent or weak (Pola & Wyatt, 1991). Stimulus duration has to exceed 20ms for full processing of the velocity signal in slashed motion (Barnes & Asselman, 1992), but some small differences of smooth-pursuit and saccadic eye movements were observed even at 20ms stimulus duration, indicating that some processing or accumulation of the velocity signal occurs even at very brief target presentation.

Chapter 8

Motion sensitivity and visual tracking of continuous and apparent visual motion stimuli (Experiment 3)

The findings of Experiment 2 indicated that single-mode pursuit gain in response to apparent motion stimuli follows an inverted U-shape or band-pass function as a function of target velocity from 2.5 to 35.0 deg/s, but smooth pursuit gain for continuous motion decreases linearly with increasing target velocity. Previous research implies a possible lower velocity limit for smooth pursuit of continuous motion (Carl & Gellman, 1987; M. M. Churchland & Lisberger, 2000; Spering et al., 2005), although this has not been explicitly reported in the literature. Furthermore, the results from Experiments 1 and 2 have demonstrated that if such a velocity limit exists for smooth pursuit of continuous motion, then it is below 2.5 deg/s target speed for a small, single dot target stimulus. Research on visual motion perception has shown that band-pass functions underlie many motion perception tasks, as shown in the contrast sensitivity of different spatial frequencies as a function of temporal frequency (R. L. De Valois & De Valois, 1988). Therefore, the presence of a similar function for smooth pursuit eye movements would be consistent with the more recent proposal that there are shared inputs into motion perception and smooth pursuit eye movements (which is outlined in Chapter 5), and this is supported by the findings for single-mode pursuit of apparent motion in Experiment 2, but not for continuous motion at the examined target velocities. There is very compelling evidence in support of this view, including strong psychophysical and behavioural similarities for motion perception and smooth pursuit for continuous (Beutter & Stone, 1998, 2000;

Braun et al., 2006; Krauzlis & Adler, 2001; Krauzlis & Stone, 1999; Newsome et al., 1989; Osborne et al., 2005; Stone et al., 2000; Stone & Krauzlis, 2003), and apparent motion (A. K. Churchland & Lisberger, 2001; Madelain & Krauzlis, 2003). Motion perception and smooth pursuit also have similar patterns with regard to direction discrimination (Watamaniuk & Heinen, 1999), velocity discrimination (Gegenfurtner et al., 2003; Kowler & McKee, 1987), and decreasing contrast levels (Spering et al., 2005), and they are similarly affected by other variables, such as acceleration (Watamaniuk & Heinen, 2003) and cognitive expectations (Krauzlis & Adler, 2001). This evidence has led to the view that motion perception and smooth pursuit eye movements share neurological sites and processes (Barton, Simpson et al., 1996; Dobkins et al., 1998; Keller & Heinen, 1991; Krauzlis & Stone, 1999; Leigh & Zee, 1999; Lisberger et al., 1987). There are, however, no neuro-imaging studies that have simultaneously measured motion perception and smooth pursuit on identical tasks, and it therefore cannot be ruled out that similar but independent neurological processes underlie motion perception and smooth pursuit eye movement (e.g., Goodale & Milner, 1992). In conclusion, the available evidence indicates that there is a link between motion perception and smooth pursuit eye movement and that they share some neural motion processing mechanisms and signals (e.g., Beutter & Stone, 2000), but this view is not yet generally accepted.

The view that motion perception and pursuit have shared inputs has been proposed despite the fact that smooth pursuit eye movements and motion perception have quite different functional patterns with increasing target velocity. As outlined in Chapter 5, motion sensitivity of continuous motion follows a band-pass or inverted U-shaped function as a function of target velocity, with lower motion sensitivity at both high

and low target speeds (e.g., Lankheet et al., 2000), and its peaks and upper and lower limits are at different target velocities depending on stimulus size (Bonnet, 1980), spatial frequency (Burr, 1991; Burr & Ross, 1982), and contrast (e.g., Johnston & Wright, 1985; McKee & Watamaniuk, 1994) of the target, as well as motion amplitude and duration (Bonnet, 1980; Post et al., 1984). Depending on these variables, motion can be perceived for target speeds as low as 0.02-1.00 deg/s (Johansson, 1978; Smith, 1991) and as fast as 100.0 (Burr, 1991) or even 10,000.0 deg/s (Burr & Ross, 1982). Smooth pursuit eye movements are also affected by stimulus size (Leigh & Zee, 1999), contrast (Lisberger & Westbrook, 1985; Spering et al., 2005; Tychsen & Lisberger, 1986), and the amplitude of the motion trajectory (Leigh & Zee, 1999), but the most important factor affecting single-mode pursuit performance is target velocity (Ciuffreda & Tannen, 1995; Collewijn & Tamminga, 1984; Lisberger et al., 1987; Lisberger & Westbrook, 1985; Meyer et al., 1985; Schalen, 1980; Tychsen & Lisberger, 1986).

Unlike motion perception, the performance of single-mode pursuit as a function of target velocity has invariably been described as linear. Optimal smooth pursuit eye movements are believed to be generated at slow target velocities, with decreasing performance with increasing target speed, until an upper velocity limit of smooth pursuit is reached. With respect to this upper limit there is a consensus that single-mode pursuit with velocities up to 30.0-40.0 deg/s is quite accurate but becomes increasingly inaccurate at faster velocities (see Lisberger, Morris, & Tychsen, 1987; Pola & Wyatt, 1991). The upper limit of pursuit varies greatly between individuals and can be as fast as 80.0-180.0deg/s for large target stimuli (Buizza & Ramat, 2005; Lisberger et al., 1981; Meyer et al., 1985), but it comes at a cost in accuracy and more

frequent saccades (Lisberger, Morris & Tychsen, 1987). It has been suggested that theoretically, a lower velocity limit would exist for smooth pursuit of apparent motion stimuli (Lamontagne, 1973), based on the idea that slow target speeds would not supply sufficient sample-points within a certain time period to initiate and maintain smooth pursuit eye movements, and this is consistent with findings of Experiment 2. A lower velocity limit of single-mode pursuit has not been investigated for continuous motion, despite the findings of some studies suggesting that smooth pursuit eye movements may deteriorate at very slow target speeds (Carl & Gellman, 1987; M. M. Churchland & Lisberger, 2000; Spering et al., 2005). The findings from Experiment 2 have demonstrated that single-mode pursuit of apparent motion follows an inverted U-shape with both upper and lower velocity limits, which depend on stimulus duration and spatial separation. More specifically, similar to motion perception of apparent motion, the optimal target velocities for single-mode pursuit performance varied depending on spatial separation, stimulus duration and the type of apparent motion. Peak gain for smooth pursuit eye movements was at higher target velocities for larger spatial separations, and in addition, the single-mode pursuit peak gain for jumping-dot motion shifted to faster target speeds with increasing stimulus duration, but for slashed motion, peak pursuit gain shifted to slower target speeds with increasing stimulus duration. Because continuous motion can be conceptualised as a slashed motion stimulus with extended stimulus duration, it is conceivable that smooth pursuit gain in response to continuous motion also follows a band-pass function, with its peak at very slow target speeds but this has not actually been tested. If there is indeed a strong link or shared inputs to motion perception and smooth pursuit, one would expect similar functions for motion sensitivity and single-mode

pursuit gain under the same experimental conditions, not only for apparent, but also for continuous motion.

Most of the studies that have investigated motion sensitivity to date have used spatial frequency gratings, the sensitivity of which are determined for a much larger area than a single dot, or they have examined global motion processing or short-range motion, using random-dot kinematograms. In comparison, most experiments examining smooth pursuit eye movements employ a smaller local motion stimulus, such as a single dot target, which covers a greater spatial distance, and as mentioned previously, little data is available on the motion sensitivity of such targets. Watamaniuk and Heinen (1999) compared smooth pursuit in response to both single dots and random-dot targets and found pursuit to be very similar, which suggests that motion sensitivity data from random-dot displays may apply to smooth pursuit of single dot targets, but a direct comparison for the same tasks is more valid. One of the few studies that has investigated motion perception of a single dot was that of Westheimer and Wehrhahn (1994), revealing that direction discrimination was very accurate for a single dot and concluding that directional processing for motion and the general detection of an object's orientation in space share the same underlying processing mechanisms. Furthermore, Geisler (1999) investigated luminance detection thresholds for moving single dots and found that single dots in continuous motion produce a motion 'streak' (or 'smear') at fast target velocities due to the visual persistence that accompanies temporal integration. Such a motion smear has also been found at low luminance levels (Pashkam & Cavanagh, 2007), when visual persistence is also high (Di Lollo & Bishof, 1995). This motion smear is believed to provide spatial cues to the direction of the motion and thus improve motion detection

for both single dots (Geisler, 1999) and random-dot displays (Edwards & Crane, 2007; Tong, Aydin, & Bedell, 2007). Others, however, have proposed that the perception of single-dots decreases at fast velocities, because the motion smear decreases the stimulus contrast (Westheimer & Wehrhahn, 1994). The existence of a motion smear for single-dot targets is another reason why a direct comparison of motion perception and smooth pursuit is more valid when similar stimuli are used.

In summary, the aim of the present study is to further investigate the proposed link between motion perception and smooth pursuit eye movements by directly comparing smooth pursuit eye movements and motion sensitivity for the direction of motion for continuous, slashed and jumping-dot motion stimuli at a wide range of target speeds. Although a lot is individually known about motion sensitivity and smooth pursuit, and there is some evidence that they share underlying processes, the two have not yet been directly compared using a single dot motion stimulus for continuous and apparent motion. A second aim of the present study is to identify whether single-mode pursuit of continuous motion stimuli has a lower velocity limit, and whether it also follows an inverted U-shape or band-pass function as a function of target velocity, similar to that found for apparent motion in Experiment 2.

Based on the findings from motion sensitivity studies and studies of smooth pursuit outlined above the following hypotheses are proposed:

1. Motion sensitivity for all motion stimuli is expected to follow a quadratic (band-pass) function as a function of target velocity (e.g., Lankheet et al., 2000).

2. Peak sensitivity for the apparent motion stimuli is expected to be at faster target velocity than for continuous motion, because apparent motion can be perceived at higher velocities than continuous motion under the same viewing conditions (L. Kaufman et al., 1971).
3. Single-mode pursuit gain for apparent motion stimuli is expected to follow a quadratic function, with reduced gain at both slow and fast target velocities, as was found in Experiment 2.
4. If perception and pursuit of continuous and apparent motion stimuli have shared inputs it is expected that motion sensitivity and single-mode pursuit gain will have similar functional patterns as a function of target velocity, with peaks at similar target speeds.
5. Finally, the findings regarding dual-mode visual tracking and both single-mode pursuit and saccadic variables are expected to replicate the findings from Experiment 2.

Method

Participants

There were five male and seven female participants (mean age 21.0 years, *SD*=3.1), meeting the same inclusion criteria reported in Experiments 1 and 2 (detailed in the *Method* section of Experiment 1), and one participant in this study had also taken part in Experiment 1. Written informed consent was obtained and the study had approval from the *Tasmanian Social Science Human Research Ethics Committee.*

Motion stimuli

Continuous, slashed and jumping-dot motion stimuli were generated as detailed in Experiment 2, but the apparent motion stimuli were presented at only one stimulus duration (60ms) and one spatial separation (2.0 deg), based on findings of Experiment 2. Stimulus duration of 60ms was selected to allow time for the velocity signal in slashed motion to be fully processed, while still allowing a large range of target speeds (see Chapter 7). A spatial separation of 2.0 deg was chosen, because findings in Experiment 2 indicated this to be the smallest spatial separation producing significant effects. All paradigms were presented at 11 constant velocities (1.0, 2.0, 4.0, 6.0, 8.0, 10.0, 12.0, 14.0, 18.0, 22.0, 24.0 deg/s), with apparent motion calculated as detailed in Experiment 2. The current study placed emphasis on slow target speeds as these have not commonly been examined in the available literature to date, and findings of Experiments 1 and 2 demonstrated the need to include stimulus velocities below 2.5 deg/s in order to further investigate the possibility of a lower velocity limit to smooth pursuit.

For the motion sensitivity task, the motion stimulus was presented horizontally, moving randomly left-to-right or right-to-left over a 6.0 deg spatial trajectory. The target characteristics were chosen so that they were consistent with most of the small group of similar motion perception tasks available in the literature and similar to these studies, the spatial motion trajectory was kept constant, even though this resulted in different temporal exposures for different target speeds. The spatial trajectory was set at 6.0 deg, because this represents the smallest spatial distance allowing four target presentations per stimulus velocity, and larger spatial windows

resulted in very long exposure times at slow target speeds with the inherent problem that participants could use uncontrolled cognitive strategies to detect motion direction, a problem identified during pilot testing. The motion always crossed the centre of the screen, but to minimise the use of potential cognitive strategies (e.g., focusing on end-point of spatial window) the movement was initiated randomly within 0.0-2.0 deg of the centre point. Initiating the motion stimulus at random points resulted in the target motion also finishing at random locations, therefore controlling for participants' using the detection of the stimulus motion starting- or endpoint location to complete the task. Furthermore, participants were instructed to fixate on the centre location and wait for the motion to cross the centre location.

Direction threshold was measured using a directional two-alternative forced-choice (2-AFC) procedure (D. M. Green & Swets, 1966) with a modified staircase. With their chin on a chin-rest at a distance of 1.0 m from the monitor, participants were instructed to focus on the centre of the screen and identify the direction of the target motion (right-to-left or left-to-right) using a response pad. A modified staircase procedure was then used to identify the threshold contrast level for the detection of the direction of the movement. The staircase used eight staircase reversals, with the criterion for a staircase reversal being three consecutive correct responses for contrast decrease, and one error for contrast increase, which estimated the 79.4% correct level of response on a psychometric function (Wetherill & Levitt, 1965). The stimulus was first presented at 10 % (Michelson) contrast level, which was well above threshold for all participants. After each three consecutively correct responses, contrast was decreased by a 1.5 dB step for the first three staircase reversals, and was further reduced in steps of 0.75 dB for the last five reversals. Only the last three staircase

reversals were used to calculate the contrast threshold and sensitivity values for each condition.

Procedure

Data was collected in one session lasting between 60 to 90 minutes, which was interrupted with regular rest breaks. The motion perception and visual tracking tasks and the three types of motion stimuli were presented in alternating order to minimise order effects. For the motion perception task, the stimulus velocities were presented in randomised order, but because of constraints of the visual tracking software, targets for visual tracking were presented in order from slowest to fastest target speed.

Eye Movement Recording

The eye movements were recorded in the same way as detailed in Chapter 6.

Eye Movement Analysis

Eye movements were analysed in the same way as detailed in Chapter 6.

Measures

Motion sensitivity (1/ contrast of direction threshold) was measured for the motion perception task. Direction and velocity are the most basic determinants of motion (Westheimer & Wehrhahn, 1994), and sensitivity to the detection of the *direction*, rather than detection of motion was selected. This ensured that actual motion was perceived rather than simply measuring object detection (Bonnet, 1980; Burr & Ross, 1982), although the thresholds for detection of the stimulus and identification of its direction are often similar for achromatic motion (Dobkins & Albright, 1998; Smith, 1994b). For the eye movement task, the same measures were used as in Experiment 2.

Data Analysis

As no significant effects were found Experiment 1 for direction of eye tracking in regards to patterns of effects, eye movement data for right- and leftward tracking was collapsed for all analyses. 3 [Type of Motion: Continuous, Jumping-dot, Slashed] X 11 [Target Velocity: 1.0, 2.0, 4.0, 6.0, 8.0, 10.0, 12.0, 14.0, 18.0, 22.0, 24.0 deg/s] repeated measures ANOVAs with Greenhouse-Geisser corrections were conducted for all measures and significant main effects for type of motion were followed up with one-way repeated measures ANOVAs and pairwise comparisons for Type of Motion averaged for all target speeds. Significant effects of target velocity were investigated using within-subjects contrasts (to check for linearity), and significant interactions between Type of Motion and Target Velocity were followed up using separate ANOVAs and pairwise comparisons to compare the three motion stimuli at each target velocity. Bonferroni-adjusted alpha levels were used for multiple comparisons.

Results

An overall 3 [Type of Motion: Continuous, Jumping-dot, Slashed] X 11 [Target Velocity: 1.0, 2.0, 4.0, 6.0, 8.0, 10.0, 12.0, 14.0, 18.0, 22.0, 24.0 deg/s] repeated measures ANOVA was conducted for each dependent variable and the results are summarised in Table 9.

Table 9. Summary of results of Type of Motion X Target Velocity ANOVAs for motion sensitivity and visual tracking (including smooth pursuit and saccadic eye movements)

Measure	Main Effect of Type of Motion	Main Effect of Target Velocity	Motion X Velocity Interaction
Motion Perception			
Motion Sensitivity	**$F(1,15)=194.6,\eta^2=.95$*****	**$F(3,28)=53.1,\eta^2=.83$*****	**$F(3,32)=39.3,\eta^2=.78$*****
Dual-Mode Tracking			
Dual-Mode Eye Velocity	$F(2,19)=1.2,\eta^2=.11$	**$F(2,17)=427.2,\eta^2=.98$*****	$F(3,28)=1.0,\eta^2=.09$
Dual-Mode Gain	$F(2,15)=0.3,\eta^2=.00$	$F(4,37)=0.6,\eta^2=.06$	$F(5,46)=0.5,\eta^2=.05$
Single-Mode Pursuit			
Single-Mode Eye Velocity	**$F(1,2)=14.3,\eta^2=.61$****	**$F(2,20)=156.2,\eta^2=.95$*****	$F(4,32)=2.4,\eta^2=.21$
Single-Mode Gain	**$F(1,11)=32.9,\eta^2=.79$*****	**$F(3,30)=4.7,\eta^2=.34$****	**$F(5,47)=5.6,\eta^2=.38$*****
Saccades			
Saccade Frequency per Second	**$F(2,20)=52.6,\eta^2=.84$*****	**$F(2,21)=58.2,\eta^2=.85$*****	$F(5,51)=2.3,\eta^2=.19$
Saccade Frequency per Cycle	**$F(2,20)=88.2,\eta^2=.89$*****	**$F(1,15)=42.8,\eta^2=.80$*****	**$F(3,38)=8.9,\eta^2=.45$*****
Saccade Amplitude	$F(1,12)=4.1,\eta^2=.27$^	**$F(2,22)=45.6,\eta^2=.81$*****	$F(4,44)=1.3,\eta^2=.11$
Saccade Duration	**$F(2,18)=4.3,\eta^2=.28$***	**$F(2,25)=30.0,\eta^2=.73$*****	$F(4,41)=0.8,\eta^2=.07$
Saccade Peak Velocity	**$F(1,14)=4.5,\eta^2=.31$***	**$F(3,31)=25.8,\eta^2=.72$*****	$F(6,59)=1.6,\eta^2=.14$
Time-based Saccade Ratio	**$F(2,18)=17.5,\eta^2=.64$*****	**$F(3,26)=48.3,\eta^2=.83$*****	$F(3,34)=0.7,\eta^2=.06$
Distance-based Saccade Ratio	**$F(2,18)=11.7,\eta^2=.54$****	**$F(1,11)=7.8,\eta^2=.44$***	$F(2,20)=3.2,\eta^2=.24$^

Note: ^p=.06, *p<.05, ** p<.01, *** p<.001; significant effects are in bold.

Motion sensitivity to continuous and apparent motion stimuli

There were significant main effects of type of motion and target velocity on motion sensitivity, as well as a significant interaction (Table 9). Motion sensitivity was significantly higher for continuous motion than for jumping-dot and slashed motion. The interaction between type of motion and target velocity was followed-up with separate one-way repeated measures ANOVAs comparing motion sensitivity to the three motion stimuli at each target speed. As illustrated in Figure 43a, motion sensitivity for continuous motion was significantly higher than for both types of apparent motion stimuli only for target speeds up to 18.0 deg/s.

The best fit for continuous motion sensitivity as a function of target velocity was for a linear trend [$F(1,11)=120.5$, $p<.001$,$\eta^2=.92$], although the data could also be fitted with higher order trends (cubic and higher) with large effect sizes ($\eta^2=.64$-$.78$). The linear trend clearly relates to the motion sensitivity function for target speeds of 2.0 deg and more, with highest motion sensitivity at 2.0 deg/s target velocity, and a linear decrease in sensitivity with increasing target velocity. It is important to note, however, that motion sensitivity was much lower at 1.0 deg/s target speed (see Figure 43a), which explains the significant higher order trends. But because there are not sufficient data points at slow target velocities, it is not possible to draw a valid conclusion about the shape of the function. Motion sensitivity to both slashed [$F(1,11)=53.4$, $p<.001$,$\eta^2=.83$] and jumping-dot [$F(1,11)=21.7$, $p<.01$,$\eta^2=.66$] motion as a function of target velocity best fitted quadratic trends (Figure 43b). Peak motion sensitivity for slashed motion was at 6.0 deg/s target speed, while the function for jumping-dot motion exhibited a flatter, less well defined peak with highest motion sensitivity around 10.0-14.0 deg/s target velocity. This means that motion sensitivity as a function of target velocity has an optimal velocity, which depends on the type of motion stimulus and decreases for target speeds below and above this optimum.

In order to further examine the significant interaction between the type of motion and target velocity a repeated measures ANOVA was conducted comparing only the two apparent motion paradigms across target velocity. This analysis revealed a significant interaction between the type of apparent motion and target speed [$F(5,52)=11.6$, $p<.001$,$\eta^2=.51$]. Pairwise comparisons between jumping-dot and slashed motion (using Bonferroni-adjusted $\alpha=.0045$) showed that motion sensitivity to slashed

motion was only significantly higher than for jumping-dot motion for target velocities of 2.0-6.0 deg/s, while at 22.0 deg/s target speed the reverse was the case (see Figure 43b). This pattern of results and the shape of the functions strongly suggest that motion sensitivity for the two apparent motion paradigms represent band-pass functions with peaks at different target speeds.

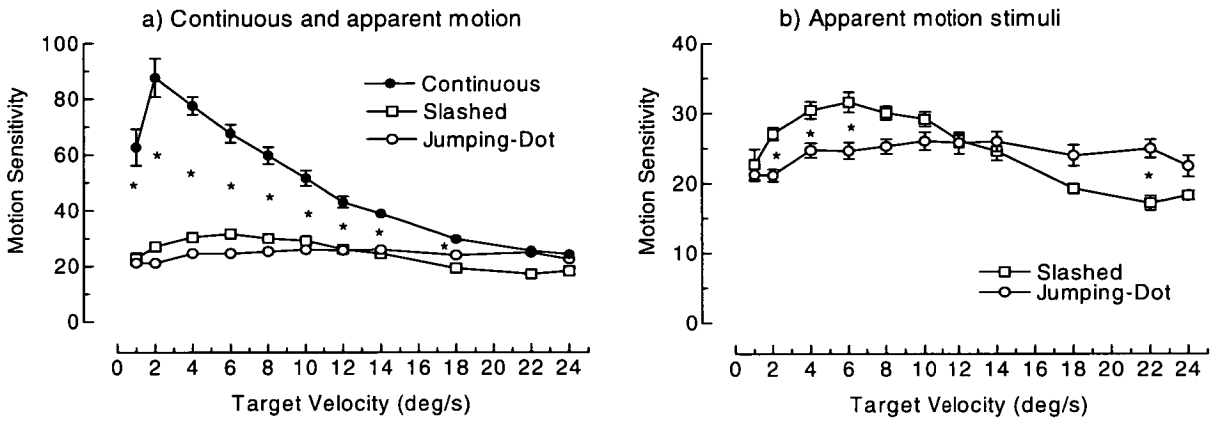

Figure 43. Motion sensitivity for continuous, slashed, and jumping-dot motion as a function of target velocity for a) all three motion stimuli and b) apparent motion only on a smaller scale. * denote significant differences, $p<.0045$; error bars depict standard errors of the mean (*SE*).

Visual tracking of continuous and apparent motion stimuli

Dual-mode tracking

Dual-mode eye velocity increased linearly with increasing target velocity but there were no differences in dual-mode eye velocity or gain in response to the three types of motion (Table 9 and Figure 44), consistent with the findings of Experiment 2. These findings again show that when smooth pursuit and saccadic eye movements are combined in visual tracking, apparently moving stimuli are tracked as well as continuous motion stimuli.

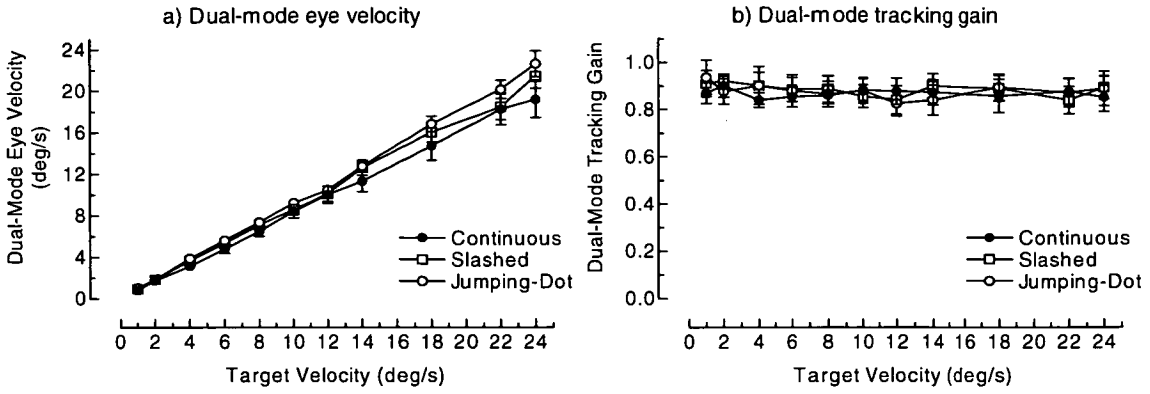

Figure 44. Dual-mode (a) eye velocity and (b) gain for the visual tracking of continuous, slashed and jumping-dot motion (error bars depict *SE*).

Single-mode pursuit

Single-mode pursuit eye velocity increased significantly with increasing target velocity for all three types of motion (Table 9), and there was a significant effect of the type of motion, which was followed up using a one-way ANOVA comparing mean pursuit eye velocity for the three motion stimuli averaged for all target speeds (followed by pairwise comparisons of the three means, α=.016). This revealed that single-mode pursuit eye velocity in response to jumping-dot motion was significantly slower than in response to continuous and slashed motion, but pursuit eye velocity elicited by continuous and slashed motion did not differ significantly (see Figure 45a).

For single-mode pursuit gain there were significant main effects for type of motion and target velocity, but there was also a significant interaction (Table 9). This interaction was followed up using separate repeated measures ANOVAs comparing the three types of motion at each target velocity, followed by paired-sample t-tests (α=.0045). As illustrated in Figure 45b, differences in single-mode pursuit gain in response to the three types of motion were only significant for target velocities below

18.0 deg/s. Single-mode pursuit gain elicited by jumping-dot motion was significantly lower than for continuous and slashed motion up to a speed of 14.0 deg/s, with the exception of 1.0 deg/s target speed, where visual tracking of both types of apparent motion stimuli contained virtually no smooth pursuit. Also, single-mode pursuit gain in response to continuous motion was significantly better than for slashed motion only at 1.0 and 2.0 deg/s target velocity. For faster speeds pursuit gain was similar for continuous and slashed motion.

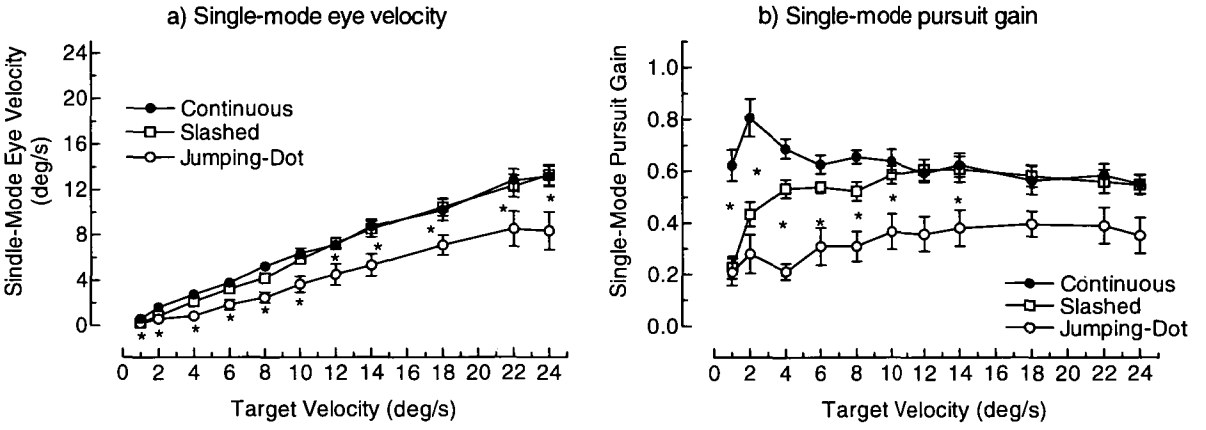

Figure 45. Single-mode pursuit (a) eye velocity and (b) gain for continuous, slashed and jumping-dot motion (* denote significant differences between motion stimuli, (a) $p<.016$, (b) $p<.0045$; error bars depict *SE*).

Single-mode pursuit gain in response to continuous motion only fitted a significant quintic trend as a function of target velocity, and peak pursuit gain was at 2.0 deg/s target speed. Single-mode pursuit gain decreased when target velocity was slower or faster than 2.0 deg/s, similar to the function found for motion sensitivity. Single-mode pursuit gain for slashed motion followed a quadratic trend [$F(1,11)=27.4$, $p<.001, \eta^2=.71$], with peak pursuit performance at 12.0-14.0 deg/s target velocity, while single-mode pursuit gain for jumping-dot motion best fitted a linear trend

[$F(1,11)=11.5$, $p<.01$,$\eta^2=.56$] and had less well defined a peak around 18.0-22.0 deg/s.

Frequency of saccades

The number of saccades generated per second increased significantly with increasing target velocity (Figure 46). There was also a significant main effect of the type of motion (Table 9), which was followed-up using a one-way ANOVA comparing the mean number of saccades per second for the three motion stimuli, averaged for all target speeds, followed by pairwise comparisons ($\alpha=.016$). These analyses revealed that significantly more saccades were generated per second during the tracking of apparent motion stimuli than continuous motion, and there were significantly more saccades per second in response to jumping-dot than slashed motion (see Figure 46).

The number of saccades made per cycle decreased significantly with increasing target velocity, as was found in Experiments 1 and 2. A significant interaction between the type of motion and target velocity (see Table 9) was followed up with separate ANOVAs comparing the three motion stimuli at each target velocity, followed by pairwise comparisons (Bonferroni-adjusted $\alpha=.0045$). As illustrated in Figure 46, there were significantly more saccades per cycle when tracking apparent motion stimuli than for continuous motion, but there was no difference between jumping-dot and slashed motion. These differences in saccade frequency between continuous and apparent motion were larger at slow target velocities, and decreased with increasing target velocity until there were no longer any differences when target speed exceeded 12.0 deg/s.

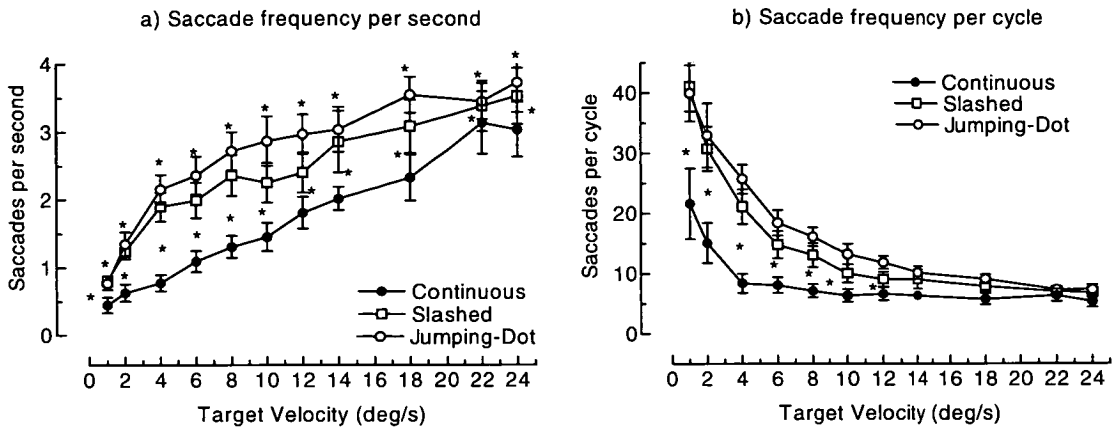

Figure 46. Saccade frequency per (a) second and (b) cycle (note that these are on different scales). * denote significant differences between motion stimuli, (a) $p<.017$ and (b) $p<.0045$; error bars depict *SE*.

Characteristics of saccades

Saccade amplitude, duration, and peak velocity increased significantly with increasing target speed for all three types of motion (Table 9; Figure 47). Consistent with the findings of Experiments 1 and 2, a larger number of saccades of smaller size, duration and peak velocity covered the spatial trajectory at slow target velocities, whereas at faster target speeds, a smaller number of larger, and faster saccades of longer duration were generated.

The significant main effects of type of motion for saccade duration and peak velocity (see Table 9) were followed-up with one-way ANOVAs comparing means for the three motion stimuli (averaged for target velocity), followed by pairwise comparisons ($\alpha=.016$). These revealed that saccade duration in the tracking of jumping-dot stimuli had a tendency to be longer than for continuous and slashed motion stimuli (although this only reached $p=.03$), and saccade peak velocity was significantly slower when tracking continuous than jumping-dot motion stimuli (as shown in Figure 47). For saccade amplitude there was only a trend towards statistical significance for

differences between the three motion tasks (p=.06), with a tendency for larger saccades for continuous than apparent motion stimuli.

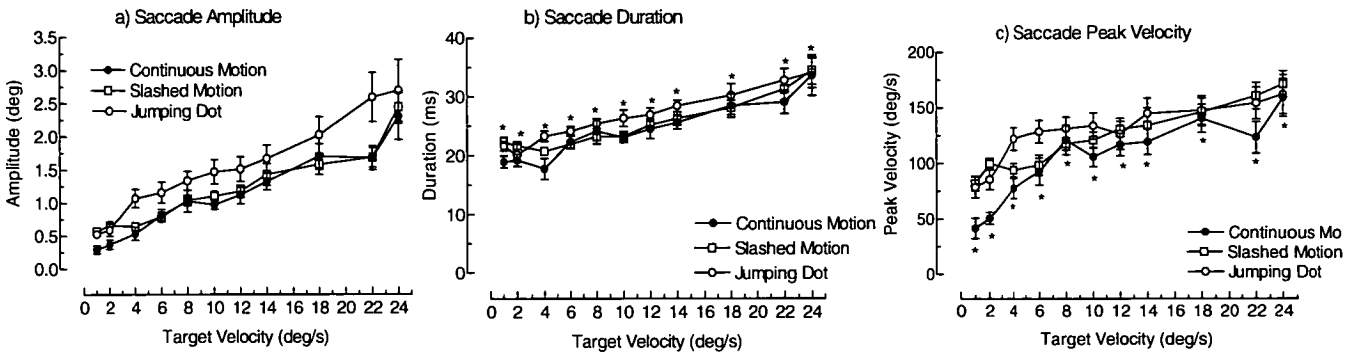

Figure 47. Saccade characteristics as a function of target velocity for saccade (a) amplitude, (b) duration and (c) peak velocity in the tracking of continuous, slashed and jumping-dot motion (* denote significant main effect of type of motion stimuli, p<.05; error bars depict *SE).*

Ratio of saccadic versus pursuit eye movements

The time-based and distance-based ratios of saccadic versus pursuit eye movements had quite different functions with increasing target speed (see Figure 48), as was found in Experiments 1 and 2. The duration of time spent in saccadic versus pursuit eye movements increased with increasing target velocity and depended on the type of motion stimulus (see Table 9). One-way ANOVAs comparing the three types of motion stimuli (followed by pairwise comparisons) revealed that the time-based saccade ratio was larger in response to apparent motion, but it suggests a very small saccadic contribution to visual tracking (Figure 48a). This is inconsistent with the available data from other smooth pursuit and saccadic variables, and the visual traces (see Figure 49), which all show very low single-mode pursuit gain and a large number of saccades at slow target speeds.

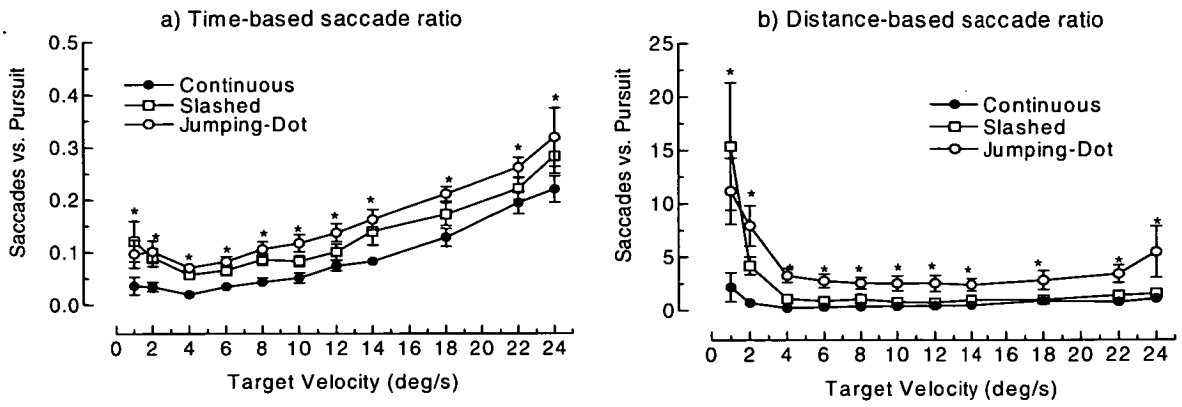

Figure 48. Ratio of (a) time and (b) distance covered by saccadic versus pursuit eye movements as a function of target velocity in the tracking of continuous, slashed and jumping-dot motion (note that they are on different scales). * denote significant differences between motion stimuli ($p<.017$); error bars depict *SE*.

In contrast, the ratio of spatial distance covered by saccadic versus smooth pursuit eye movements indicates a much larger contribution of saccadic eye movements to dual-mode tracking than the time-based ratio data would suggest. The significant main effect of type of motion (Table 9) was followed-up with a one-way repeated measures ANOVA comparing the mean distance-based ratio averaged for all target speeds and pairwise comparisons ($\alpha=.016$). These revealed that visual tracking of the two apparent motion stimuli had a significantly higher spatial saccadic contribution than continuous motion, and the interaction between the type of motion and target velocity was close to significance ($p=.06$). As illustrated in Figure 48b, at slow target speeds the saccadic contributions were similar when tracking the two apparent motion stimuli, while at faster target speeds slashed motion was more similar to continuous motion.

Summary of visual tracking of continuous and apparent motion stimuli

For all three types of motion stimuli, single-mode pursuit gain was lower at 1.0 deg/s target speed. In particular in response to the two apparent motion stimuli there was

virtually no smooth pursuit at 1.0 deg/s target speed and a large number of small, slow saccades of short duration covered the majority of the trajectory. The eye traces presented in Figure 49 illustrate this and also show that for all three types of motion the frequency of saccades per cycle and the ratio of saccadic eye movements gradually decrease with increasing target velocity as the visual tracking trace becomes smoother. Once target speed exceeds the optimal velocity for peak smooth pursuit gain (which depends on the type of motion stimulus) single-mode pursuit gain decreases again and visual tracking is supplemented by a smaller number of large and fast saccades of long duration.

This pattern is evident for all three types of motion stimuli, although it is much more pronounced for visual tracking of apparent motion. When comparing visual tracking of the three types of stimuli single-mode pursuit of jumping-dot motion had the lowest gain, supplemented by the largest saccadic contribution, with more frequent, faster and temporally longer saccades. Visual tracking of continuous motion had the smallest saccadic contribution, with higher single-mode pursuit gain, and for slashed motion, single-mode pursuit and saccadic measure were at intermediate levels. Any differences in smooth pursuit and saccadic eye movements between the three motion stimuli were much more pronounced at slow target velocities, and this is also illustrated in Figure 49.

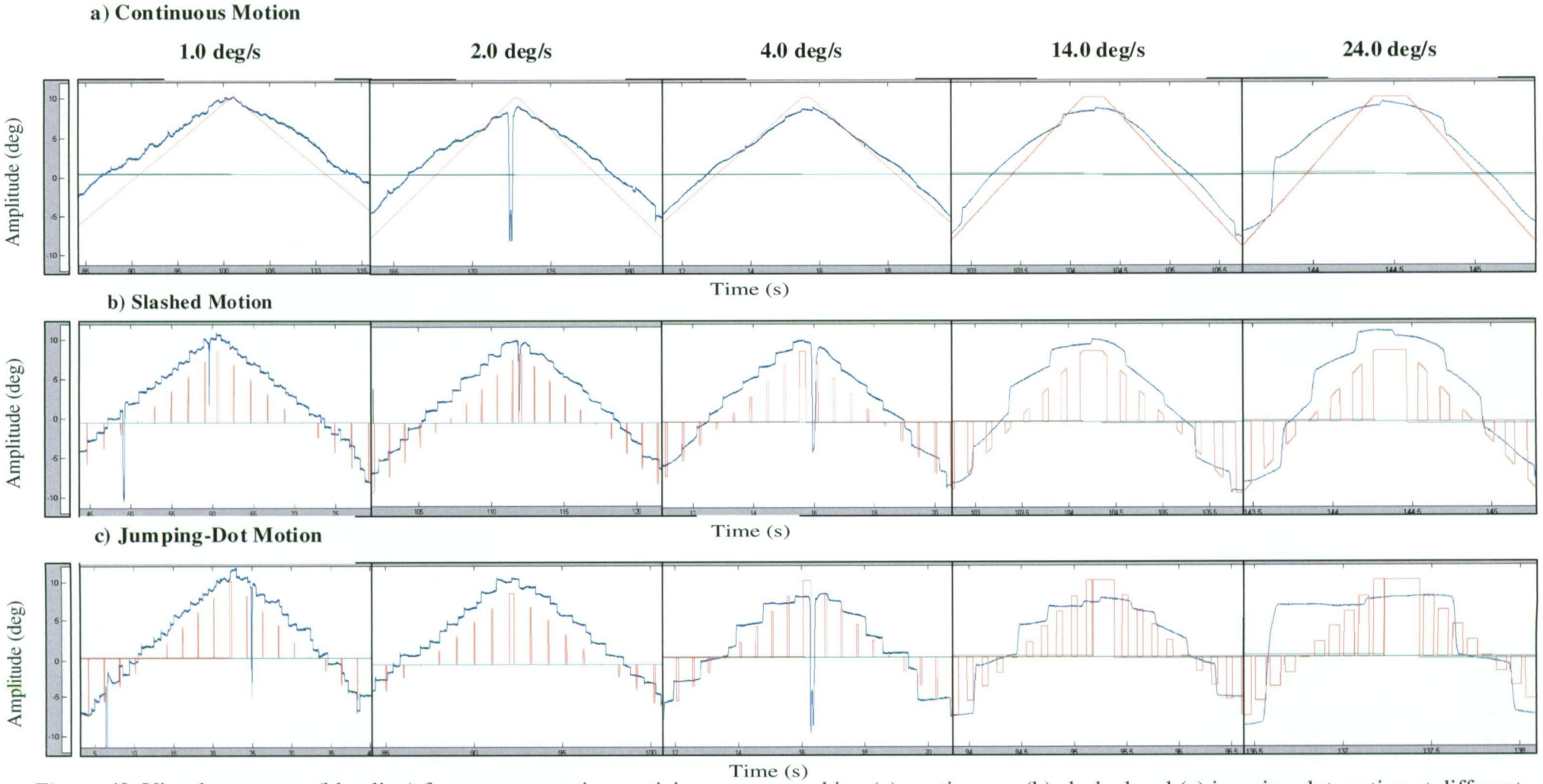

Figure 49. Visual eye traces (blue line) for a representative participant (SM) tracking (a) continuous, (b) slashed and (c) jumping-dot motion at different target speeds (red line/bars represent the target stimulus).

Discussion

The results of Experiment 3 revealed important findings in relation to motion sensitivity and visual tracking of continuous and apparent motion stimuli. These findings will first be discussed individually for motion sensitivity and visual tracking, followed by a discussion of the similarities and differences between motion sensitivity and single-mode pursuit gain for continuous and apparent motion stimuli.

Motion sensitivity of continuous and apparent motion stimuli

A comparison of motion sensitivity of continuous and apparent motion

The present study measured motion sensitivity of continuous, slashed and jumping-dot motion stimuli for a single dot. As was hypothesised on the basis of the motion perception literature (e.g., Lankheet et al., 2000), an inverted U-shape pattern resembling a band-pass function was found for motion sensitivity as a function of target velocity for all three motion stimuli, but with peak sensitivity at different target velocities. Motion sensitivity for the three motion stimuli was rather low in the present study, with peak sensitivity for continuous motion below values generally reported for random dot kinematogramsor spatial frequency gratings (Bonnet, 1980) because of the small size and high spatial frequency (Bonnet, 1980; Burr, 1991; Burr & Ross, 1982) of the single-dot target stimulus. As predicted, motion sensitivity of continuous motion was significantly higher than for both types of apparent motion, demonstrating superior visual motion processing for continuous than apparent motion stimuli, while the overall magnitude of motion sensitivity for jumping-dot and slashed motion was similar. The perception of motion relies on the integration of signals over

space and time and motion detectors have a specific spatial distribution and specific time delays between them (Snowden & Braddick, 1989a). Continuous motion stimuli provide an unlimited number of sampling-points over the course of the motion trajectory and this therefore facilitates motion perception. In contrast, apparent motion stimuli provide significantly fewer sampling points, and how 'continuous' the apparent motion is perceived depends primarily on spatio-temporal factors, such as temporal separation, spatial separation and stimulus intensity (Korte, 1915; Neuhaus, 1930; Wertheimer, 1912). Unless these parameters perfectly match the distribution and time delays of the receptors, the visual system is less sensitive to these types of stimuli.

The inverted U-shape function as a function of target velocity found for motion sensitivity of continuous and apparent motion stimuli showed a decrease in motion sensitivity at both slow and fast target velocities. The functions for apparent motion stimuli best fitted quadratic trends, but the motion sensitivity function for continuous motion was less well defined, fitting linear as well as higher order trends with high effects sizes. It is most likely that the target speeds investigated in the current study do not provide sufficient data points for stimulus velocities below peak sensitivity to properly identify the shape of the motion sensitivity function. Nevertheless, the motion sensitivity data in the present study demonstrates that motion sensitivity for both continuous and apparent motion stimuli peaks at a preferred target velocity and decreases for target speeds above and below this optimal velocity.

A comparison of the motion sensitivity peaks for continuous, slashed, and jumping-dot motion stimuli

The motion sensitivity functions for continuous, slashed and jumping-dot motion as a function of target velocity are band-pass, with peak sensitivity at different target velocities. For continuous motion stimuli the peak of the motion sensitivity function was found to be at target velocity of 2.0 deg/s, although motion was still perceived at 1.0 deg/s target velocity, consistent with previous reports (Johansson, 1978; Smith, 1991). Peak motion sensitivity for the apparent motion stimuli was at significantly faster target velocities than for continuous motion, and these findings are also related to spatio-temporal integration. When there is a spatial gap between successive targets, as is the case in apparent motion, the visual perception of motion is enhanced by increasing the stimulus velocity for two main reasons: First, the temporal delay between successive stimulation of spatially distant receptors is shorter at faster target speeds, which improves the integration of the signal across these receptors. Second, with increasing target velocity, the number of presentations *within a specific sampling period* also increases, which results in higher motion sensitivty, because motion perception is enhanced by the number of successive presentations over time (Snowden & Braddick, 1989a). In contrast, the continuous motion stimulus has no spatial gap and provides an unlimited number of sample-points, which means that even at slow target velocities, motion can be perceived. Furthermore, peak sensitivity for jumping-dot motion was at slightly faster target velocities than for slashed motion stimuli, and this effect can be explained by the additional velocity signal available in slashed motion. Slashed motion includes a velocity signal with each target presentation, and the accumulation of this velocity signal with successive target

presentations (Barnes & Asselman, 1992), enhances spatio-temporal integration and peak motion sensitivity is therefore at slower target velocities for slashed than jumping-dot motion.

Visual tracking of continuous and apparent motion stimuli

Findings that replicate the results of Experiment 2 in regards to visual tracking of continuous and apparent motion stimuli

The data for the visual tracking of continuous and apparent motion stimuli replicated many of the findings of Experiment 2 in regards to dual-mode tracking and individual single-mode pursuit and saccadic variables. First, dual-mode tracking was not affected by the type of motion stimulus, although tracking of the different stimuli was accomplished with different combinations of saccadic and smooth pursuit eye movements. Second, single-mode pursuit gain in response to continuous motion was superior to that elicited by apparent motion, particularly at slow target speeds, and saccades contributed to a much larger extent to dual-mode tracking of apparent than continuous motion. Third, differences in single-mode pursuit and saccadic measures were again found between jumping-dot and slashed motion, but these were more pronounced in the present study than in Experiment 2, which can be explained by the fact that apparent motion paradigms in the present study were presented at 60ms target exposure, while many of the analyses in Experiment 2 were conducted at 20ms stimulus duration. This finding lends further support to the view proposed by Barnes and Asselman (1992) that adequate processing of the velocity signal in slashed motion only occurs for stimulus durations exceeding 30ms, although the fact that some differences were found even at 20ms stimulus duration in Experiment 2 shows that some processing of the velocity signal occurs even when stimulus duration is

below 30ms, at least over successive presentations. Fourth, the current results replicated the significant contribution of saccades to dual-mode tracking at both slow and fast target velocities, with the present results again demonstrating that a large number of smaller, slower, and temporally shorter saccades cover the spatial trajectory at slower target speeds, and a smaller number of larger, faster, and temporally longer saccades are generated at fast target speeds, this effect being much stronger for apparent motion. The interpretation of the different measures of saccadic eye movements again suggested that time-based measures of saccadic frequency and saccadic ratio are not valid measures of the saccadic tracking component, because time-based measures (e.g., Avila et al., 2003; Avila, Weiler et al., 2002) are affected by overall crossing time, the inherent dynamics of the saccadic and smooth pursuit eye movements, and the changes in saccade dynamics with increasing target velocity. Interpreting the distance-based ratio of saccades (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999) in combination with saccade frequency per spatial unit and broad saccade characteristics (such as amplitude) provides the most accurate estimate of the saccadic contribution to visual tracking.

Findings that extend the results of Experiment 2 in regards to visual tracking of continuous and apparent motion stimuli

The findings of Experiment 2 were extended in the present study by including target velocities as low as 1.0 deg/s, which revealed that single-mode pursuit of continuous motion stimuli decreased at slower stimulus velocity, and single-mode pursuit gain was much lower at 1.0 deg/s target velocity. A similar decrease in single-mode pursuit gain for target velocities below optimal velocity was found for both jumping-

dot and slashed motion stimuli in the present study and in Experiment 2, demonstrating that single-mode pursuit gain for apparent motion follows a band-pass function with increasing target velocity. The findings of the present study demonstrate that smooth pursuit for continuous motion also follows an inverted U-shape function, which strongly suggests that smooth-pursuit eye movements in response to continuous and apparent motion stimuli are generated in a similar way, although the differences in the stimuli result in different optimal velocities for peak single-mode pursuit gain. Peak single-mode pursuit gain for jumping-dot motion was at fastest target velocity (18.0-22.0 deg/s), and peak gain for slashed motion was at slower target speeds (12.0-14.0 deg/s) because of the additional velocity signal available in slashed motion stimuli. Also, findings of Experiment 2 demonstrated that for slashed motion, optimal stimulus velocity for peak single-mode pursuit gain shifted to slower target velocities with increasing stimulus duration. The present finding that peak single-mode pursuit gain in response to continuous motion stimuli was at 2.0 deg/s target velocity is consistent with the idea that the peak for continuous motion is simply shifted to slower target speeds. This further suggests that the continuous, slashed and apparent motion stimuli are not completely different types of motion, but that they can be conceptualised on a continuum, with jumping-dot motion providing the least amount of information to the visual system (position information only), slashed motion providing an added velocity signal, and continuous motion extending the velocity signal to longer stimulus duration.

Direct comparison of motion sensitivity and single-mode pursuit eye movements

Similarities between motion sensitivity and single-mode pursuit

A number of significant similarities are observed when directly comparing the functions for motion sensitivity and single-mode pursuit gain as a function of target velocity for the three types of motion stimuli. First, motion sensitivity and single-mode pursuit gain of continuous motion have a very similar functional pattern as a function of target velocity, with peaks at the optimal stimulus velocity of 2.0 deg/s. Both motion sensitivity and single-mode pursuit gain of continuous motion decrease significantly when target velocity is below the optimal target speed of 2.0 deg/s, with significantly lower peak sensitivity and single-mode pursuit gain at 1.0 deg/s target speed. This not only demonstrates that both motion perception and smooth pursuit of continuous motion have a lower velocity limit, but that this limit is at the same stimulus velocity. This provides direct support for the view that motion perception and smooth pursuit eye movements for continuous motion stimuli have shared inputs, as has been previously suggested (see Chapter 5).

Second, both motion sensitivity and single-mode pursuit gain of jumping-dot and slashed motion stimuli follow a quadratic function with increasing target velocity, and for both the motion sensitivity and single-mode pursuit gain functions the peak for jumping-dot motion is at faster target velocities than for slashed motion stimuli. This provides direct support for the view that motion perception and smooth pursuit eye movements have shared inputs also in response to apparent motion stimuli.

Third, the performance of both motion sensitivity and single-mode pursuit gain is significantly better in response to continuous than apparent motion stimuli for slow target velocities, but at fast target velocities (above 14.0-18.0 deg/s) there are no longer any significant differences between the three types of motion. This provides further evidence for shared inputs into motion perception and pursuit. The large differences between the three motion stimuli at slow target velocity for both motion sensitivity and single-mode pursuit gain are a result of their differences in the lower velocity limits and optimal velocities for peak performance. This suggests that any study comparing the perception or pursuit of the three motion stimuli needs to include slower target velocities (i.e., below 15.0deg/s) to capture these differences. The lack of significant differences between the three motion stimuli at fast target velocities suggests that for both motion sensitivity and smooth pursuit there is an upper velocity threshold at which the sampling rate of apparent motion approximates that of continuous motion and spatio-temporal integration for continuous and apparent motion is therefore similar.

A fourth similarity between motion sensitivity and single-mode pursuit gain is that they both decrease for all three motion stimuli at slow target velocities. When stimulus velocity is slower than optimal target velocity for a given motion stimulus motion sensitivity is low, because the target velocities do not support the spatio-temporal integration of motion signals across motion detectors with their spatial distributions and inherent time delays (Snowden & Braddick, 1989a). The motion stimulus is therefore not sufficient to appropriately engage motion perception mechanisms (Smith, 1991). The fact that single-mode pursuit gain decreases at slow target velocities in a similar way to motion sensitivity suggests that they rely on

spatio-temporal integration across motion receptors in a similar way: single-mode pursuit gain at slow target velocities is low because the smooth pursuit system is not sufficiently engaged just as motion perception mechanisms are not fully engaged at the same target velocities. Lamontagne (1973) suggested a theoretical lower limit for single-mode pursuit in response to apparent motion stimuli when the flash rate is so low that it no longer permits continuous tracking with smooth eye movements, but he never tested this empirically. Such a lower limit for apparent motion would theoretically be reached at slower target velocities when spatial separation is decreased, because smaller spatial separations result in a higher flash rate for a given target velocity, and this was indeed found in Experiment 2 for both apparent motion stimuli. Based on this idea it follows logically that continuous motion also has a lower velocity limit, but because the spatial separation is reduced to zero the flash rate is unlimited and the velocity limit is therefore shifted to much slower target velocities, which is indeed what was found in the present experiment.

These similarities between motion sensitivity and single-mode pursuit gain in the present study provide strong evidence for shared inputs into motion perception and smooth pursuit eye movements, relying on the same processes of spatio-temporal integration across motion detectors. This is consistent with existing evidence that motion perception and smooth pursuit have similar patterns with regard to discrimination of direction (Watamaniuk & Heinen, 1999) and velocity (Gegenfurtner et al., 2003; Kowler & McKee, 1987). Watamaniuk and Heinen (1999) measured smooth pursuit to both single dot and random-dot targets and found these to be very similar to each other and to perceptual direction discrimination. Such behavioural experiments, like these cited studies and the present research, can only demonstrate

the similarities between motion perception and smooth pursuit and not directly rule out that the two merely have very similar but independent underlying processes and mechanisms (e.g., Goodale & Milner, 1992). However, all current evidence, including neuro-imaging studies and the present findings, have clearly established the strong similarities and overlap in the pathways and performance of motion perception and pursuit systems and the most parsimonious explanation for these many similarities is certainly that motion perception and smooth pursuit have shared inputs.

Differences between motion sensitivity and single-mode pursuit eye movements

Despite many similarities between motion sensitivity and single-mode pursuit gain in the current study there were also two main differences: First, the motion sensitivity functions exhibited much more clearly defined peaks than single-mode pursuit gain for all three motion stimuli. Second, while motion sensitivity declined in a very steep and linear fashion when target speed exceeded optimal velocity, single-mode pursuit gain declined much more gently. These differences could be interpreted as evidence against the view that motion perception and smooth pursuit have shared inputs, but there are also alternative explanations for these differences. These differences could indicate that there may be additional mechanisms that are involved in the generation of smooth pursuit eye movements, consistent with previous suggestions that although motion perception and pursuit have shared neural mechanisms pursuit eye movements may also have additional, independent mechanisms (Stone & Krauzlis, 2003). One such mechanism may be pursuit prediction, which has been shown to play a very significant role in smooth pursuit eye movements (e.g., Bahill, Iandolo, & Troost, 1980, see Chapter 2), because it enables the pursuit system to use information about past motion (Stark et al., 1962) to increases accuracy of smooth pursuit (Bahill et al.,

1980; Dodge et al., 1930), and to anticipate changes in the position or velocity of a target (Boman & Hotson, 1992; Kowler & Steinman, 1979). In the present study, eye movement stimuli were presented over three cycles (a total of 120.0 deg), which allows sufficient time for prediction mechanisms to be activated and anticipate the motion and velocity of the target for medium to high velocities. For target velocities below optimal velocity for peak single-mode pursuit gain prediction is likely to be weak or absent, because smooth pursuit is not fully engaged, but at optimal target velocity and beyond, when smooth pursuit is fully engaged, prediction mechanisms enhance single-mode pursuit, therefore enabling it to maintain a relatively high level of single-mode pursuit gain despite motion sensitivity deteriorating at similar target speeds. Another explanation for the relatively gentle decline in single-mode pursuit gain at fast target velocities compared with the sharp deterioration in motion sensitivity relates to target presentation. The visual perception of motion has been shown to benefit from additional information received from integration over multiple successive presentations of the target over *space*, up to at least six presentations (Snowden & Braddick, 1989b). In the present study the motion sensitivity task was restricted to four target exposures over the spatial trajectory, because they were presented only for a 6.0 deg trajectory, and in contrast, the visual tracking target had many more presentations, because it was presented for three full cycles (120.0 deg). Furthermore, directional motion detection for both continuous and apparent motion is enhanced by temporal integration over *time* (Snowden & Braddick, 1989a; Sperling, 1976) up to at least 300ms (Sekuler et al., 1990). In the present study, the motion sensitivity target was presented for durations below 300ms (ranging from approximately 25-200ms) for target velocities exceeding 8.0 deg/s, and durations for the visual tracking task were much longer than 300ms at the same target velocities.

This can also explain why single-mode pursuit gain did not deteriorate to the same degree as motion sensitivity when target speed exceeded optimal velocity. Finally, these differences between motion sensitivity and single-mode pursuit gain could be because motion sensitivity was investigated using a contrast sensitivity task, and the stimuli for motion perception were therefore presented at or below contrast threshold levels, while the stimuli for visual tracking were presented above contrast threshold. Motion sensitivity improves with increases in contrast (Edwards & Badcock, 1996; Johnston & Wright, 1985), although this effect is stronger for slow target velocities (Blakemore & Snowden, 1999), and these differences in contrast between the motion sensitivity and visual tracking tasks may have contributed to the differences in the functions for motion sensitivity and single-mode pursuit gain.

Behavioural experiments measuring task performance on motion perception and smooth pursuit tasks, such as the current study, will always be limited somewhat by some task differences, even if these are minimised. Despite identical motion parameters, the differences between the perception and pursuit tasks in the current study were still significant, which limits the interpretation of differences in performance. Measuring task performance with simultaneous behavioural experiments of pursuit and perception (such as by Stone & Krauzlis, 2003) could be a way around this. Although these types of experiments are not without difficulties (see Stone & Krauzlis, 2003), they do eliminate any variation due to task differences and extending such an approach to using both continuous and apparent motion stimuli is recommended. However, measuring perception and pursuit on identical tasks does restrict the types of tasks that can be used, and typically very simple motion perception judgement tasks are used (e.g., Stone & Krauzlis, 2003). It is possible to

measure the visual tracking performance during the motion perception task employed in the current study, although this would compare open-loop, rather than closed-loop pursuit performance.

Values of the motion sensitivity and single-mode pursuit gain functions

The absolute values for the peaks and upper and lower limits for motion sensitivity and single-mode pursuit gain reported here should not be interpreted as absolute values. There are many other factors that affect motion sensitivity and single-mode pursuit gain, including the size and spatial frequency of the target, viewing distance, luminance etc. (see Chapter 5). Henderson (1971) suggested that for motion perception there is effectively no lower limit to the velocity that will allow motion discrimination, provided target exposure is sufficiently long. Upper velocity limits for smooth pursuit (Meyer et al., 1985) and motion perception (Burr & Ross, 1982) have been shown to increase dramatically for very large target stimuli. The absolute values for motion sensitivity and single-mode pursuit gain would therefore be expected to shift to slower or faster target speeds, depending on these variables, but the general pattern as a function of stimulus velocity for each task would stay the same. In the present study, at the parameters investigated, motion sensitivity and single-mode pursuit gain in response to continuous motion displayed peaks at a very slow target speeds, but the examined velocity range was still able to capture that there is a lower velocity limit for motion sensitivity and single-mode pursuit gain. The examined velocity range did not supply a sufficient number of data points to adequately measure the shape of the function at slow target speeds though and did therefore not show the expected quadratic or inverted U-shape function found for apparent motion stimuli. It would be useful to repeat the study measuring a greater number of target

velocities within the lower velocity range (i.e., 0.5-5.0 deg/s) and with equal differences between the measured velocities. Alternatively, the experimental conditions could be adjusted in a way that will shift peak motion sensitivity and single-mode pursuit gain for continuous motion to faster target velocities, for example by decreasing background luminance or the spatial frequency of the target. These adjustments to the experimental parameters may facilitate finding a more clearly quadratic band-pass function for continuous motion, if indeed present, as was found for the two apparent motion stimuli.

Perceived motion smear for a single-dot stimulus

Participants reported that they perceived a motion smear at fast target velocities for both the motion perception and visual tracking tasks and researchers could clearly observe such motion streak during data collection for all three experiments. Such a motion smear has previously been described for single-dot stimuli, and there is some evidence that this motion smear enhances motion perception at faster target speeds (Edwards & Crane, 2007; Geisler, 1999; Tong et al., 2007). Geisler (1999) proposed that motion perception at slower target speeds is based on more accurate estimates of velocity components, and only when these become less reliable at faster target velocities does the visual system increasingly rely on estimates based on the orientation of the motion streak. In contrast, Westheimer and Wehrhahn (1994) suggested that the motion streak actually decreases motion perception for a single-dot, because they result in the dot looking more like a line, therefore making it a low-contrast stimulus. Although, if this is the case, the fact that the single-dot is perceived like a line would also reduce the spatial frequency of the stimulus and increase its size, which both enhance motion sensitivity. Nevertheless, because the motion smear

was present equally for both the motion perception and the visual tracking tasks the comparisons between the two are still valid.

Summary and conclusions

The present study aimed to further investigate the proposed link between motion perception and smooth pursuit eye movements. It also aimed to identify whether single-mode pursuit elicited by continuous motion stimuli follows a band-pass function with increasing target velocity, with upper and lower velocity limits, similar to that found for apparent motion in Experiment 2. The present experiment replicated findings from Experiment 2 with regard to dual-mode tracking and its single-mode and saccadic components in response to continuous and apparent motion stimuli, but it also extended these findings. The present study demonstrated that single-mode pursuit gain in response to continuous motion follows an inverted U-shape pattern resembling a band-pass function with increasing target velocity, with peak single-mode pursuit gain at a slower target speed than for apparent motion stimuli. This strongly suggests that the same mechanisms underlie smooth pursuit eye movements in response to continuous and apparent motion stimuli. A direct comparison of the functions for motion sensitivity and single-mode pursuit gain as a function of target velocity revealed many similarities that provided support for the view that motion perception and smooth pursuit eye movements have shared inputs. Both motion sensitivity and single-mode pursuit gain displayed decreased performance at slow target speed for all three motion stimuli and superior performance in response to continuous compared to apparent motion stimuli at slow target velocities. Also, peak performance for both motion sensitivity and single-mode pursuit gain was at fastest target speed for jumping-dot stimuli (18.0-22.0 deg/s), and at slightly slower speeds

for slashed motion (12.0-14.0 deg/s), with continuous motion displaying peak sensitivity and gain at very slow target velocities (2.0 deg/s). This is consistent with the idea that the three motion stimuli are on a continuum of motion energy. Continuous motion provides an unlimited number of sample-points conveying both position- and velocity-signals, slashed motion provides a limited number of sample-points for both position- and velocity-signals, and jumping-dot stimuli provide a limited number of sample-points for position-information only.

The data also revealed differences between motion sensitivity and single-mode pursuit gain, with more clearly defined peaks and a steeper decline in motion sensitivity than for single-mode pursuit gain. These differences are likely to be due to prediction, which enhances single-mode pursuit eye movements but not motion sensitivity when the pursuit system is engaged. Other factors that may have contributed to these differences between motion sensitivity and single-mode pursuit gain are small differences between the motion stimuli for motion perception and visual tracking; a smaller motion trajectory and lower contrast for motion sensitivity task. It is concluded that the present findings strongly support the view that motion perception and smooth pursuit eye movements have shared inputs.

Chapter 9

General discussion

The aims of this thesis were to investigate the specific roles and contributions of saccadic and smooth pursuit eye movements to the visual tracking of continuous and apparent motion stimuli and to examine the relationship between visual motion perception and visual tracking. Three experiments were conducted: Experiment 1 (Chapter 6) examined the visual tracking of continuous motion over a wide range of target speeds. It aimed to quantify visual tracking of a single-dot in continuous motion and to evaluate the different measures that have been used to describe the saccadic tracking component. A significant saccadic contribution to visual tracking was apparent at all target velocities and the measure of the ratio of distance covered by saccadic versus pursuit eye movements was identified as the preferred measure of the saccadic tracking component. Experiment 2 (Chapter 7) investigated the visual tracking of slashed and jumping-dot apparent motion stimuli and compared them to the tracking of continuous motion. This experiment aimed to examine the interplay of saccadic and smooth pursuit eye movements during visual tracking and the spatio-temporal stimulus conditions that result in each type of eye movement response. Single-mode pursuit gain elicited by continuous motion was shown to decrease linearly with increasing target speed, in conjunction with a parallel increase in the saccadic contribution. In contrast, single-mode pursuit gain of apparent motion displayed a quadratic band-pass function with increasing target velocity with the peak gain of this function depending on spatial separation, stimulus duration, and the type of apparent motion stimulus. The findings also revealed that at target velocities below

the peak of smooth pursuit gain a large number of small saccadic eye movements were generated. In contrast, at target speeds above the peak of the smooth pursuit function, a smaller number of larger, faster, and temporally longer saccades were produced. Experiment 3 (Chapter 8) aimed to extend the velocity range in order to further investigate single-mode pursuit gain of continuous motion and to compare visual tracking eye movements to visual motion perception under similar experimental conditions. The experiment demonstrated that single-mode pursuit gain for continuous motion also has a lower velocity limit, similar to what was found in response to apparent motion. More specifically, single-mode pursuit gain in response to both continuous and apparent motion stimuli follow an inverted U-shaped (band-pass) function with increasing stimulus velocity. The inverted U-shape functions found for single-mode pursuit gain and motion sensitivity were highly similar in response to both continuous and apparent motion stimuli with increasing target velocity, with similar functional shapes and peaks. This finding supports the view that visual motion perception and smooth pursuit eye movements may have shared visual inputs. The present chapter discusses the findings of all three experiments in the context of the overall aims of the thesis.

The spatio-temporal parameters for smooth pursuit and saccadic eye movements in visual tracking

This thesis has revealed that smooth pursuit and saccadic tracking eye movements depend on spatio-temporal stimulus parameters of the target stimulus mediated by target velocity. The focus of this section is the nature of the functions of smooth pursuit gain and the contribution of saccadic eye movements to visual tracking with

increasing stimulus velocity and their relationship to possible mechanisms underlying these functions.

Smooth pursuit eye movements in visual tracking with increasing target velocity

The quality of the performance of smooth pursuit eye movements depends on the velocity of the target stimulus. The previous literature reports that smooth pursuit eye movements are specialised for slowly moving targets (e.g., Lisberger et al., 1987) and that the quality this performance decreases linearly with increasing target speed, by becoming gradually less accurate at faster velocities (e.g., R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Lisberger et al., 1987; Pola & Wyatt, 1991). In contrast, the current results suggest that smooth pursuit eye movements have an optimal target velocity, which depends on the type of motion and its characteristics (such as spatial separation and stimulus duration). The performance of single-mode smooth pursuit gain decreases linearly when target velocity exceeds this optimal velocity, as was previously suggested, but it is important to note that it also declines when target speed decreases *below* the optimal velocity for a given stimulus.

The reason that this finding has not been reported in previous studies is most likely because the target velocity for optimal smooth-pursuit eye movements elicited by continuous motion is generally very low. Previous experiments have examined visual tracking of continuous motion with target speeds of 5.0 deg/s and above, and in this velocity range smooth pursuit gain does indeed decline linearly as a function of target velocity. The few studies that have investigated slower target speeds have found a deterioration of smooth pursuit at slow target velocities. Murphy (1978) reported that single-mode pursuit gain decreased for one of two observer for target velocity below

1.0 deg/s and Carl and Gellman (1987) reported that target velocities below 5.0 deg/s were associated with slower pursuit acceleration and significantly higher latencies. Spering, Kerzel, Braun, Hawken, and Gegenfurtner (2005) found slower pursuit acceleration, higher latencies, lower gain and larger position errors at 1.0 deg/s than at faster target velocities, and Churchland and Lisberger (2000) had to exclude data for the visual tracking of apparent motion in monkeys when target velocity was lower than 2.0 deg/s, because the eye tracking traces were too variable and contained too many saccades to conduct a reliable and valid analysis. These reports are consistent with the current finding of a deterioration of single-mode pursuit gain at slow target velocities and support the idea that single-mode pursuit gain follows a band-pass function. Furthermore, the optimal pursuit performance roughly corresponds to the range of target speeds represented in area MT for motion perception (A. K. Churchland et al., 2005; Gegenfurtner & Hawken, 1995; Newsome et al., 1986). This is consistent with the idea of shared inputs for motion perception and smooth pursuit eye movements.

The spatio-temporal parameters for optimal performance of smooth pursuit eye movements

The inverted U-shape function of single-mode pursuit gain as a function of target velocity peaks at an optimal target velocity, which in turn depends on the spatio-temporal parameters of the stimulus. It has previously been reported that the performance of smooth pursuit eye movements depends on the contrast (Lisberger & Westbrook, 1985; Spering et al., 2005; Tychsen & Lisberger, 1986), and size (Leigh & Zee, 1999) of the target stimulus as well as its background (Collewijn & Tamminga, 1984; Kowler et al., 1978; Spering & Gegenfurtner, 2007a; Wyatt et al.,

1994; R. D. Yee et al., 1983). The current findings show that in addition to these variables, the type of motion of the target stimulus and its spatio-temporal characteristics also affect smooth pursuit eye movements. Peak single-mode pursuit gain for apparent motion stimuli is found at faster target velocities compared to that for continuous motion, because when an apparent motion stimulus moves at faster velocities it provides a greater number of sample-points within a given timeframe than when it moves slowly. Increasing the number of target presentations enhances smooth pursuit in a similar way that multiple presentations over space and time improve the perception of apparent motion (Snowden & Braddick, 1989a, 1989b). This also explains why the preferred velocity for single-mode pursuit gain shifts to faster target velocities when spatial separation are larger in apparent motion. Faster target velocities also reduce the temporal delay between the successive stimulation of spatially distant receptors, which also explains why optimal target velocities are faster when spatial separations are large. The stimulus duration of each target presentation for apparent motion stimuli also affects the peak of single-mode pursuit gain for apparent motion stimuli, but differently for jumping-dot and slashed motion. Optimal pursuit performance shifts to faster target velocities when the stimulus duration increases for jumping-dot stimuli, because with each presentation of the stationary target, smooth pursuit eye velocity is 'antagonistically slowed' by the stationary signal (Barnes & Asselman, 1992, as described in Chapter 7), and faster target speeds are required to counteract this. In contrast, when stimulus duration is increased for slashed motion, peak single-mode pursuit gain shifts to slower target velocities, because the velocity signal that is available during target presentation 'synergistically enhances' pursuit eye velocity (Barnes & Asselman, 1992). Taken together, these findings suggest that the optimal target velocity for smooth pursuit eye movements,

which results in peak single-mode pursuit gain, depends on the type and spatio-temporal characteristics of the motion stimulus. Peak gain is at the target velocity that results in the optimal combination of the other parameters for spatio-temporal integration.

The decline of smooth pursuit eye movements below and above optimal pursuit velocity

Single-mode pursuit gain deteriorates when target speed is above or below the optimal target velocity for a given continuous or apparent motion stimulus. The deterioration of smooth pursuit when target speed *exceeds* optimal velocity for continuous motion stimuli has been described in the literature. The purpose of smooth pursuit eye movements is to keep a moving target foveated to allow continuous viewing of the object (R. H. S. Carpenter, 1988) and visual acuity starts to decrease when target velocity exceeds 3.0 deg/s (Westheimer & McKee, 1975). Smooth pursuit for continuous motion therefore has a relatively slow preferred velocity and single-mode pursuit gain decreases with increasing target velocity, because smooth pursuit eye movements are not able to keep up with the target (Lisberger et al., 1987). In the current experiments, differences in smooth pursuit eye movements elicited by continuous and apparent motion stimuli were no longer statistically significant once target velocity exceeded optimal pursuit velocity for the apparent motion stimulus. This indicates that there is an upper velocity threshold for smooth pursuit at which the sampling rate of apparent motion approximates that of continuous motion and the spatio-temporal integration for continuous and apparent motion is therefore similar. This further suggests that the deterioration in single-mode pursuit gain for target

speeds exceeding the optimal velocities for jumping-dot and slashed motion stimuli is probably guided by similar mechanisms to those for continuous motion.

In contrast, the deterioration of smooth pursuit eye movements at target speeds *below* optimal velocity has not been previously described for continuous or apparent motion stimuli. It was suggested by earlier authors that such a lower limit would exist for smooth pursuit of apparent motion stimuli because at slow target velocities the stimulus rate is so low that it no longer engages the pursuit system (Lamontagne, 1973). More specifically, it has been suggested that slow target speeds result in a failure of the visuo-motor drive to initiate pursuit (Churchland & Lisberger, 2000). The current findings show that such a deterioration of smooth pursuit not only occurs for apparent motion stimuli, but that single-mode pursuit gain in response to continuous motion also deteriorates when stimulus velocity is sufficiently slow. This deterioration at slow target speeds is most likely caused by a failure of the visuo-motor drive to properly initiate pursuit eye movements as a result of an insufficient motion signal. In addition, at slow target velocities the pursuit system can not use pursuit prediction based on an estimate of periodicity (Barnes et al., 1987), which may also contribute to the low pursuit gain at very slow target speeds.

Saccadic eye movements in visual tracking as a function of target velocity

Saccadic eye movements during visual tracking have been conceptualised as a consequence of single-mode pursuit deficits (M. M. Churchland & Lisberger, 2000). Because single-mode pursuit gain was believed to decrease linearly with increasing target velocity, the contribution of saccades has generally been described as a one-dimensional process of an increase in saccade frequency and amplitude with

increasing tracking velocity, aiming to compensate for reduced gain (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Hallett, 1986; Lisberger et al., 1987; Pola & Wyatt, 1991; Schalen, 1980). In contrast, the current findings demonstrate that although the contribution of saccadic eye movements to visual tracking does increase when single-mode pursuit decreases, the quality and nature of this contribution is quite different for target velocities below and above a given optimal pursuit velocity.

When target speed *exceeds* the optimal pursuit velocity for a given motion stimulus, saccadic eye movements make an increasing contribution to dual-mode visual tracking, as has been previously identified (R. H. S. Carpenter, 1988; Ciuffreda & Tannen, 1995; Hallett, 1986; Lisberger et al., 1987; Pola & Wyatt, 1991; Schalen, 1980). These saccades aim to refoveate the stimulus when the eye lags behind the target and are triggered by the retinal position error resulting from by this lag (e.g., Lisberger et al., 1987). These saccades consider the ongoing velocity of the target in their planning (e.g., Keller & Johnsen, 1990; Ron et al., 1989b), possibly by using *eye crossing time* (position error/ retinal slip; De Brouwer, Yuksel et al., 2002). The previous literature generally reports an increase in the rate of saccadic eye movements with increasing target velocity, but the findings of this thesis have demonstrated that this depends on the type of frequency measure used. Whereas the number of saccades generated in a given timeframe (e.g., per second) increases with increasing target velocity, the number of saccades generated to cover a certain spatial distance (e.g., 1.0 deg, one tracking cycle) actually *decreases* with increasing target velocity. The results of all three experiments consistently demonstrated that distance-based saccade frequency measures are more valid to assess the saccadic contribution, because time-based saccade frequency measures are more strongly affected by confounding

variables, such as the dynamics of the types of eye movements or the overall time it takes to cross the motion trajectory. The present findings indicate that a *smaller* number of saccades with greater amplitude, peak velocity, and duration are generated to cover the distance of the motion trajectory of the target when stimulus velocity increases. This is consistent with previous reports that larger position errors are required to trigger saccades at fast compared to slow tracking velocities (Collewijn & Tamminga, 1984; Gellman & Carl, 1991), and that less frequent, but significantly larger saccades are therefore produced at fast tracking speeds.

For target velocities *below* the optimal pursuit velocity for a given target stimulus the contribution of saccadic eye movements to dual-mode visual tracking also increases. An increasing number of saccades with smaller amplitude, peak velocity, and duration are generated to cover the spatial trajectory of the moving target below optimal pursuit velocity. These are not triggered by the retinal position error of the eye lagging behind the target, because smooth pursuit is not actually properly engaged under these conditions. In other words, the rule of 'eye crossing time' (De Brouwer, Yuksel et al., 2002) does not apply in this case because what we observe technically not saccades triggered during smooth pursuit, but saccadic tracking. In this case the saccades are likely to be triggered directly by the retinal position error of the image displacement, in the absence of a velocity signal, which is not actually being fully computed. For apparent motion stimuli this image displacement is the discrete target step of the stimulus, but targets moving continuously at extremely slow velocities (i.e. below 2.0 deg/s) also fail to provide sufficient sample-points within a certain time period to be integrated over space and time and are therefore also tracked as discrete displacement steps. As target speed increases smooth pursuit is

increasingly engaged and an eye velocity signal is generated, assisting in the generation of saccades, and the rule of 'eye crossing time' starts to apply.

The coordination of saccadic and smooth pursuit eye movements in visual tracking

The present series of experiments on the visual tracking of continuous and apparent motion stimuli have revealed a number of new findings with regard to the interplay of saccadic and smooth pursuit eye movements during visual tracking. This section discusses these findings and what they may reveal about the visual inputs driving saccadic and smooth pursuit eye movements and about how the two kinds of eye movements are coordinated during visual tracking.

The visual inputs into to saccadic and smooth pursuit eye movements during visual tracking

The findings of this thesis are consistent with the view that saccadic and smooth pursuit eye movements process both velocity information (retinal slip velocity) and position information (retinal image displacement), (e.g., Gardner & Lisberger, 2001; Krauzlis, 2004; Krauzlis & Stone, 1999; Orban de Xifry & Lefèvre, 2007, see also Chapter 4). This is in contrast to the traditional view, which proposed that it is the type of retinal signal that determines what kind of eye movement is generated. In the current studies, jumping-dot apparent motion with spatial separation as large as 2.0 deg, elicited single-mode pursuit eye movements that were not distinguishable from those in response to continuous motion, even though jumping-dot stimuli only provide retinal position information. Smeets and Brenner (1995) proposed that position and velocity signals are processed independently for perception and action

and the present findings support this. The additional velocity signal available in slashed motion stimuli enhanced smooth pursuit eye movements, compared with the position signal only available in jumping-dot stimuli. The magnitude of this enhancement increased with increasing exposure to the velocity signal. This suggests that position and velocity signals can be processed independently and also that both types of signals can be used by both saccadic and smooth pursuit eye movements. When both are available, position and velocity signals are combined into a spatio-temporally integrated visual motion signal (Stone et al., 2000), and the type of eye movement that is generated during visual tracking is dependent on the spatio-temporal parameters of the target. For a given set of spatio-temporal stimulus characteristics there is an optimal target velocity resulting in an optimal spatio-temporally integrated motion signal for smooth pursuit eye movements and single-mode pursuit gain decreases when target speed is below or above this velocity. Below optimal target velocity for smooth pursuit of a given target stimulus the target is tracked by an increasing number of small, slow, and brief saccades. Above optimal velocity for a given target stimulus a smaller number of saccades of greater amplitude, peak velocity, and duration are generated. This suggests that a main determinant of whether a target is tracked by smooth pursuit or saccadic eye movements is the spatio-temporal parameters of the target stimulus, including its velocity. If the stimulus parameters do not allow the integration of the position and/or velocity information across space and time to generate an actual or perceived motion signal (for example, continuous motion at extremely slow velocities, or apparent motion stimuli with large spatial separation at slow target speeds), saccades are generated as the main eye movement tracking the target. When stimulus parameters allow some spatio-temporal integration (for example, with increasing target velocity

or decreasing spatial separation for apparent motion stimuli), an actual or perceived motion signal can be computed and a combination of complementary saccadic and pursuit eye movements are produced to track the target. The extent of the contribution of each type of eye movement depends on many factors, but the smooth pursuit component does increase with increasing strength of the actual or perceived integrated motion signal.

The coordination of saccades and pursuit during visual tracking

There are three main stages of processing underlying saccadic and pursuit eye movements: visual processing, response preparation, and motor execution (Liston & Krauzlis, 2003). There is abundant evidence that saccadic and smooth pursuit eye movements share the visual processing stage, including evidence of shared visual pathways (see e.g., Fischer & Boch, 1991; Chapter 3). Additionally, there is evidence that saccadic and smooth pursuit eye movements are coordinated also at the level of response preparation through shared target selection (Case & Ferrera, 2007; Erkelens, 2006; Gardner & Lisberger, 2001, 2002; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003, 2005). Shared target selection was initially viewed as being serial in nature (Gardner & Lisberger, 2001, 2002; Schoppik & Lisberger, 2006), partly because pursuit has much shorter latency than saccades, but more recent models propose a parallel model of shared target selection (Case & Ferrera, 2007; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003, 2005). According to this view, saccadic and pursuit eye movements are both based on the same visual processing signals and they are also coordinated at the level of target selection and response preparation. At this stage, however, they have been found to respond to somewhat different criteria (Krauzlis & Dill, 2002; Liston & Krauzlis, 2005), and they differ at the motor execution level

(e.g., saccades have a longer motor time delay, Liston & Krauzlis, 2005). These more recent investigations have led to new models of the generation of saccadic and smooth pursuit eye movements that are not solely based on the type of retinal stimulus to determine the type of eye movement. Instead, they are the result of a more complex cascade of shared and coordinated sensori-motor processes (Krauzlis, 2005; Orban de Xifry & Lefèvre, 2007), including the evaluation of the sensory inputs, which can include higher order processes, such as perception and memory (Krauzlis, 2005).

The findings of the present thesis are consistent with these more recent models of the coordination of saccadic and pursuit eye movements. The present series of experiments systematically and gradually fractured the target stimulus from a continuously moving target to a pure position signal (at its most extreme the target appeared for only 20ms every 5,000ms, displaced by 5.0deg), yet, smooth pursuit and saccadic eye movements in combination maintained dual-mode tracking eye velocity and gain at very high levels. The findings of this thesis reveal that the two eye movements displayed seamless synergy; the contribution of saccadic eye movements increased gradually when smooth pursuit decreased and vice versa and are similar to findings reported by Orban de Xifry, Bennett, Lefèvre, and Barnes (2006) during target blanking. Different combinations of saccadic and pursuit eye movements of different dynamics were generated depending on the tracking conditions, with the common goal of maintaining the overall dual-mode tracking response. This is quite different from a simple 'either-or' response triggered by a retinal position or velocity signal, as traditionally suggested. Instead, it is consistent with a more dynamic model that evaluates the sensory inputs in the context of higher order processes (Krauzlis,

2005; Orban de Xifry & Lefèvre, 2007), and can generate endless combinations of saccadic and pursuit eye movements depending on the demands and dynamics of the tracking conditions.

The relationship between visual tracking and visual motion perception

The findings of the present series of experiments revealed a number of similarities between smooth pursuit eye movements and motion sensitivity to continuous and apparent motion stimuli, particularly in regard to their performance in response to different spatio-temporal parameters. The implications of these findings with regard to the relationship between visual tracking and visual motion perception are discussed in this section.

The relationship between motion sensitivity and smooth pursuit eye movements

As outlined in Chapter 5, visual motion perception and smooth pursuit eye movements have recently been proposed to share neurological sites and processes (Barton, Simpson et al., 1996; Dobkins et al., 1998; Keller & Heinen, 1991; Krauzlis & Stone, 1999; Leigh & Zee, 1999; Lisberger et al., 1987). Evidence in support of this view includes strong psychophysical and behavioural similarities for motion perception and smooth pursuit for continuous (Beutter & Stone, 1998, 2000; Braun et al., 2006; Krauzlis & Adler, 2001; Krauzlis & Stone, 1999; Newsome et al., 1989; Osborne et al., 2005; Stone et al., 2000; Stone & Krauzlis, 2003) and apparent motion (A. K. Churchland & Lisberger, 2001; Madelain & Krauzlis, 2003), similar patterns for direction discrimination (Watamaniuk & Heinen, 1999), velocity discrimination (Kowler & McKee, 1987), and decreasing contrast levels (Spering et al., 2005). They are also similarly affected by other variables, such as acceleration (Watamaniuk &

Heinen, 2003) and cognitive expectations (Krauzlis & Adler, 2001). The existing evidence indicates that visual motion perception and smooth pursuit eye movements share not only visual inputs and early visual pathways (including the retina, LGN, and V1), but also higher-level processing at the level of MT, MST and possibly further downstream (Ilg, 2008; Stone & Krauzlis, 2003), although others propose parallel, but independent processes (Gegenfurtner et al., 2003; Goodale & Milner, 1992). The similarities of the quality of motion sensitivity and single-mode pursuit gain as a function of target velocity in the present thesis suggest a very strong link between motion perception and pursuit, consistent with the view of shared processes beyond MT. Stone, Beutter, and Lorenceau (2000) concluded that smooth pursuit eye movements are not driven by retinal image motion, but a spatio-temporally integrated visual motion signal (coded in head-centric coordinates) related to object motion. The present study supports this view by demonstrating that smooth pursuit of apparent motion stimuli was driven by the perceived motion signal integrated over space and time, and it is likely that this perceived integrated visual signal was the same for both motion perception and pursuit. This strongly suggests a link between perception and pursuit beyond area MT, such as MST, because it involves processing beyond the pure retinal signal.

The relationship between motion sensitivity and saccadic eye movements

Saccades have been shown to use retinal slip velocity in their programming (Blohm et al., 2003; De Brouwer, Missal et al., 2002; De Brouwer et al., 2001; De Brouwer, Yuksel et al., 2002; Guan et al., 2005; Schreiber et al., 2006), but the relationship between motion sensitivity and saccadic eye movements is nevertheless less direct than that for smooth pursuit. Saccadic and smooth pursuit eye movements have

shared underlying visual motion processing mechanisms and are coordinated at the level of target selection (Erkelens, 2006; Gardner & Lisberger, 2001; Liston & Krauzlis, 2003). This suggests that a tight link between motion sensitivity and smooth pursuit would result in an indirect link also between motion sensitivity and saccades. However, because different decision criteria (thresholds) are used to generate saccades and smooth pursuit (Liston & Krauzlis, 2005), saccadic eye movements are increasingly involved in the visual tracking of a target when the motion signal (actual or perceived) is weak or absent, because a strong motion signal will favour the generation of smooth pursuit eye movements.

The visual tracking of continuous and apparent motion stimuli

The current thesis demonstrates that the use of apparent motion stimuli greatly enhances the understanding of visual tracking. The current findings demonstrated that the mechanisms underlying the visual tracking of continuous and apparent motion stimuli are the same, in a similar way that the visual perception of continuous and apparent motion stimuli is the same (Anstis, 1986; Braddick, 1980; Burr, 1991; Gregory & Harris, 1984; Kaneoke et al., 1997; Larsen et al., 2006; Purves et al., 1996). One of the reasons why the perception of continuous and apparent motion stimuli was originally seen as governed by different mechanisms (Anstis, 1978; M. Green & Von Grunau, 1983; Kolers, 1972, 1983) was that apparent motion can be perceived at higher velocities than continuous motion under the same viewing conditions (L. Kaufman et al., 1971). The current findings for both motion sensitivity and smooth pursuit eye movements provide an explanation for this. Continuous and apparent motion stimuli are not governed by different mechanisms, but they have

functions with different peaks with increasing target velocity, based of the spatio-temporal parameters of the stimulus. The number of sample-points provided in a given timeframe increases with increasing target velocity for apparent motion, approximating the sample rate of continuous motion at faster target velocities.

The visual perception and tracking of continuous and apparent motion stimuli are based on the same mechanisms and the findings of the current thesis suggest that continuous and apparent motion are not discrete types of stimuli, but can be conceptualised as existing on a continuum. Continuous motion provides retinal position and velocity information with an unlimited number of sample-points. Slashed motion provides retinal position and velocity information, but with a limited number of sample-points. Jumping-dot apparent motion also has a limited number of sample-points and in addition, it only provides retinal position information and a perceived velocity signal has to be generated by the visual system. The spatio-temporal parameters of apparent motion can shift the apparent motion stimuli further up or down on this continuum. For example, increasing the spatial separation for either slashed or jumping-dot motion shifts the stimulus further away from continuous motion, because it decreases the number of sample-points within a certain timeframe and/or spatial trajectory, resulting in decreased motion sensitivity and smooth pursuit gain in response to the stimulus. Similarly, increasing the stimulus duration for slashed motion shifts this stimulus more closely towards continuous motion, because continuous motion is equal to slashed motion with extended stimulus duration, which explains why increasing stimulus duration for slashed motion improves both motion sensitivity and smooth pursuit eye movements. This is consistent with models of motion perception, such as motion energy models, which

suggest that the perception of motion depends on the motion energy of a given stimulus (e.g., Adelson & Bergen, 1985; Heeger, 1987; A. B. Watson & Ahumada, 1985). The closer to continuous motion an apparent motion stimulus is on this continuum, the more spatio-temporal energy they share (Adelson & Bergen, 1985, p. 286), resulting in higher motion sensitivity and higher smooth pursuit gain in response to such a stimulus. Nevertheless, the findings of this thesis demonstrate that even highly fractured apparent motion stimuli that are on the lower end of this continuum have some motion energy and can drive smooth pursuit eye movements, albeit producing low gain. This is likely to be due to a summation of transient responses over multiple presentations, as was suggested by Barnes and Asselman (1992), for both jumping-dot (accumulation of position responses only) and slashed motion (additional accumulation of the velocity signal), until sufficient motion energy is accumulated to drive pursuit eye movements.

How best to quantify and qualify saccadic and smooth pursuit eye movements during visual tracking

Studies in the literature vary with regard to the measures they use to quantify and describe saccadic and smooth pursuit eye movements during visual tracking. This thesis evaluated different methodologies and measures, especially those used to describe the saccadic tracking component. The findings, which are discussed in this section, demonstrate the importance of choosing, specifying, and reporting what measure is being used to describe visual tracking in research studies.

Measures of smooth pursuit eye movements during visual tracking

The main measures used in the literature to quantify and qualify the smooth pursuit component of visual tracking are single-mode pursuit eye velocity and gain. Although single-mode pursuit eye velocity does *quantify* the smooth pursuit tracking component, it does not give a direct measure of the *quality* of the smooth pursuit response. In contrast, single-mode pursuit gain gives a direct estimate of how well eye velocity matches the velocity of the target, which facilitates the evaluation of smooth pursuit eye movements, particularly across a range of target velocities. For example, when visually examining a graph of single-mode pursuit eye velocity as a function of target velocity, a low gain of 0.5 is easily identified at a target speed of 20.0 deg/s, because the eye velocity (10.0 deg/s) is much smaller than the target velocity (20.0 deg/s). In contrast, a low gain of 0.5 is much more difficult to identify on the same graph at a target speed of 2.0 deg/s, because the difference between target (2.0 deg/s) and eye velocity (1.0 deg/s) appears much smaller. In other words, single-mode pursuit gain does not give different results to single-mode eye velocity, but it makes them more salient and it facilitates their interpretation and comparison with motion sensitivity.

Measures of saccadic eye movements during visual tracking

There is great variability in the types of measures that have been used in the literature to quantify and qualify the saccadic component of visual tracking. Most papers report saccade amplitude and/or saccade frequency, using a variety of frequency measures, or, in some cases, fail to specify their measure altogether (see Chapter 6). Different measures to estimate the saccadic tracking component were evaluated in the present series of studies. The findings clearly demonstrate that time-based measures of

saccadic tracking are flawed, particularly when more than one target velocity is examined. Time-based measures are not only affected by temporal characteristics of the target stimulus (including stimulus velocity) but also by the different temporal dynamics of the two types of eye movements, because saccades are inherently faster and of shorter duration than smooth pursuit eye movements. This applies particularly to measures that estimate a ratio of saccadic versus pursuit eye movements, and, as such, time-based ratios (Avila et al., 2003; Avila, Weiler et al., 2002) are not valid. A distance-based ratio, such as the ratio of spatial distance covered by saccadic versus pursuit eye movements (R.G. Ross, A. Olincy, J.G. Harris, A.D. Radant, M. Hawkins et al., 1999; Randal G. Ross et al., 1999), is clearly the best measure to *quantify* the saccadic contribution to dual-mode tracking, because it gives an estimate of the magnitude of the saccadic tracking component in comparison with the contribution of smooth pursuit eye movements. This ratio, however, does not *qualify* the saccadic contribution because the distance-based ratio of saccadic versus pursuit eye movements is similar whether the saccadic contribution consists of a large number of small saccades or a small number of large saccades. Therefore, if the nature of the saccadic tracking component is of interest, a combination of saccade frequency per spatial unit and a saccade characteristic (saccade amplitude or duration) also needs to be considered. Using these measures to estimate saccades during visual tracking will allow a more precise description of the saccadic tracking component.

Future directions

This thesis revealed a number of very important and new findings, and these findings have implications for theory and for the investigation of both normal and disordered

visual tracking. This section discusses what aspects require further investigation and clarification in normal observers, as well as the exciting possibilities that the present findings offer for future research of disordered visual tracking in psychiatric disorders, particularly in patients with schizophrenia.

Future research of visual tracking in normal observers

Band-pass function for single-mode pursuit gain in response to continuous motion

The present findings clearly demonstrate that smooth pursuit eye movements in response to continuous and apparent motion stimuli have different optimal target velocities, which depend on the spatio-temporal characteristics of the target stimulus and that smooth pursuit performance deteriorates when target speed is above or below this velocity. This strongly suggests that smooth pursuit gain and motion sensitivity have a band-pass function as a function of target velocity. An inverted U-shape quadratic function was indeed found in response to apparent motion stimuli. The functions for both motion sensitivity and single-mode pursuit gain for continuous motion stimuli clearly showed a decrease in performance for target velocities below 2.0 deg/s, but the shape of the functions were not clearly quadratic in the present study. The most likely explanation for this is that the study did not have a sufficient number of data points at the lower end of target velocities to fully capture the shape of the function. Further investigations therefore need to include a greater number of different target velocities below 5.0 deg/s, preferably with equal spacings, to capture the inverted quadratic function for continuous motion stimuli, if it is indeed present. Alternatively attempts could be made to shift the function of single-mode pursuit gain as a function of target velocity to faster target speeds by manipulating the stimulus

characteristics, such as decreasing background luminance or the spatial frequency of the target.

Shared inputs and mechanisms for saccadic and smooth pursuit eye movements and for smooth pursuit eye movements and visual motion perception

It has been suggested that the wealth of psychophysical and behavioural evidence for shared inputs into visual motion perception and smooth pursuit eye movements only provides indirect evidence for such a processing pathway (e.g., Goodale & Milner, 1992). Even though many neuro-anatomical sites have been implicated to be involved in visual motion processing and smooth pursuit eye movements, it is possible that this reflects parallel but independent pathways (Goodale & Milner, 1992), rather than shared processing. In a similar way, evidence of shared processing for saccadic and smooth pursuit eye movements could be interpreted as reflecting similar parallel, but independent pathways. Although the available evidence points against independent processes with regard to perception and smooth pursuit (e.g., Stone et al., 2000; Stone & Krauzlis, 2003), as well as saccades and smooth pursuit (Krauzlis, 2004, 2005; Krauzlis & Stone, 1999) this could be further investigated by conducting neuro-imaging studies that simultaneously measure behavioural performance and neural activity on the same tasks for both visual perception and pursuit. Similarly, studies should measure the neural activity of visual tracking of continuous and apparent motion stimuli over a large range of target velocities and compare this to the resulting different combinations of saccadic and smooth pursuit tracking components. Any changes in activity associated with changes in the contributions of each type of eye movement would indicate a change in neural activity associated with each type of eye movement, because other cognitive processes should be fairly similar across the velocity range.

The saccadic contribution to visual tracking

The present series of studies demonstrated that saccadic eye movements make a significant contribution to visual tracking at most target speeds and that the quality of the saccadic component is different for target velocities below and above optimal pursuit velocity for a given target stimulus. In the present studies saccades were not further classified into different subtypes (i.e. catch-up saccades, anticipatory saccades etc.) because the criteria for these classifications are not yet clearly established and because different subtypes have the same underlying mechanisms (Findlay & Walker, 1999; Hallett, 1986) and neurological pathways (Hepp et al., 1989), despite some differences in dynamics. Nevertheless, future research can apply the current methodology of quantifying and qualifying saccades in visual tracking to different saccade types. The present thesis has demonstrated a more dynamic saccadic contribution than the one-dimensional process previously described in the literature, which suggested a simple increase in saccade frequency and size with increasing target velocity. Further sub-classifications of saccades may reveal different saccade types underlying the saccadic contribution at slow and fast target speeds. For example, the smaller number of large saccades at fast target speeds would be expected to consist predominantly of catch-up saccades, because this type of saccades generally results from the eye lagging behind the target. In contrast to a predominance of anticipatory saccades would be expected at lower target velocities, because of their predictive nature (Van Gelder et al., 1990).

Future research of disordered visual tracking

This thesis has clearly demonstrated the great potential that apparent motion paradigms have in the investigation of visual tracking because they allow the systematic and gradual breakdown of the motion signal and the separation of position and velocity signals driving saccadic and smooth pursuit eye movements. This has particular relevance to the study of disordered visual tracking. Abnormal eye movements are found in many conditions, such including individuals who are human immunodeficiency virus (HIV)-positive (Sweeney et al., 1991), have Parkinson's disease (Leigh & Zee, 1999), or various psychiatric illnesses, including obsessive-compulsive disorder, affective disorders (Kathmann, Hochrein, Uwer, & Bondy, 2003; Lencer, Trillenberg et al., 2004; Sweeney et al., 1999), and bipolar disorder (Tien, Ross, Pearlson, & Strauss, 1996). The most widely studied area of abnormal eye movements, however, is the visual tracking deficit in observers with schizophrenia. The reason for this interest is the potential of this research to uncover the underlying neuropathology of schizophrenia (K.-H. Lee & Williams, 2000), assist with classification (e.g., K. H. Lee et al., 2001), and even be a biological marker for the disease (Calkins et al., 2008; Clementz & Sweeney, 1990; K.-H. Lee & Williams, 2000; R. G. Ross et al., 2002).

The visual tracking deficits in observers with schizophrenia mainly consist of decreased and more variable smooth pursuit gain and more frequent (Levy et al., 2000; Radant & Hommer, 1992; Sweeney, Clementz, Haas, Escobar, & et al., 1994) and larger saccades (D. E. Ross et al., 1997; D. E. Ross et al., 1998). An increased number of intrusive saccades (Levy et al., 2000), and anticipatory saccades (Randal

G. Ross et al., 1999; R. G. Ross et al., 2001), smooth pursuit initiation deficits (Clementz & McDowell, 1994; Clementz et al., 1995), and postsaccadic slowing (Lencer, Trillenberg et al., 2004) have also been reported (for reviews see Holzman, Chen, Nakayama, Levy, & Matthysse, 1998; Levy, Holzman, Matthysse, & Mendell, 1993; MacAvoy & Bruce, 1995). In particular, the phase lag (Iacono & Koenig, 1983; MacAvoy & Bruce, 1995), and increased frequency for both intrusive and catch-up saccades (Sweeney et al., 1994) have been identified as unique to schizophrenia and not found in other psychiatric disorders or people abusing substances (Radant & Hommer, 1992). Because increased saccadic frequency has been reported as one of the main features of disordered tracking in schizophrenia (S. B. Hutton & Kennard, 1998; O'Driscoll & Callahan, 2008; R. G. Ross et al., 2002), the findings of the current thesis about the way to quantify and qualify the saccadic tracking component are of particular importance in the study of the tracking deficit in schizophrenia.

Despite the fact that abnormal tracking in schizophrenia is frequently called a 'smooth-pursuit' dysfunction, the nature and location of the tracking deficit has not yet been established. Currently, there are multiple explanations for the abnormal visual tracking in schizophrenia, with one of the main questions relating to whether the tracking deficits are caused by deficiencies in the pursuit or the saccadic system. One explanation is that the smooth pursuit eye movement system is affected in schizophrenia (e.g., Sweeney et al., 1994; Sweeney et al., 1998), resulting in low gain, which in turn causes the saccadic system to generate more catch-up saccades in an attempt to compensate. Another view is that the saccadic system is affected in schizophrenia (Hommer, Clem, Litman, & Pickar, 1991; Levin, 1982; R. G. Ross et al., 1998; Van Gelder et al., 1990) resulting in a higher number of intrusive or

inaccurate saccades. Others have suggested that both systems exhibit functional deficits (Levy et al., 2000). Alternative explanations for the visual tracking dysfunction are that the deficit results from impaired interactions between the pursuit and saccadic systems (Lencer, Trillenberg et al., 2004), deficient attentional capacity (Hintze, Kühn-Dymecka, Bembenek, Wrońska, & Wciórka, 2006; Van Gelder et al., 1990; C. M. Yee, Nuechterlein, & Dawson, 1998), impaired spatial working memory processes (Kelemen et al., 2007), or reflect difficulties in processing extraretinal signals and therefore abnormal predictive pursuit (Avila et al., 2006; Avila, Hong, & Thaker, 2002; Hong et al., 2003; Hong et al., 2008; Thaker et al., 2003). A further proposed explanation for abnormal tracking in schizophrenia is that the tracking dysfunction actually reflects a motion processing deficit (Holzman et al., 1998). Evidence in support of this notion comes from studies showing that observers with schizophrenia have significantly increased motion perception thresholds (Slaghuis et al., 2005; Slaghuis, Hawkes, Holthouse, & Bruno, 2007b; Wertheim, Vangelder, Peselow, & Cohen, 1985), and this elevated threshold is correlated with smooth pursuit performance (Stuve et al., 1997). Observers with schizophrenia also exhibit lower sensitivity for direction discrimination (Tadin et al., 2006) and velocity discrimination (Chen, Palafox et al., 1999; Clementz, McDowell, & Dobkins, 2007) and this velocity discrimination deficit is also correlated with smooth pursuit performance (Chen, Levy et al., 1999). Furthermore, weakened centre-surround interactions have been found in visual motion processing of observers with schizophrenia (Tadin et al., 2006). Others argue that retinal motion perception is normal, but subsequent processing of extra-retinal motion is abnormal (Avila et al., 2006; Hong et al., 2005; Thaker et al., 1999). First degree relatives, however, generally do not show a motion perception deficit (Chen, Bidwell, & Holzman,

2005), and saccade parameters to moving targets during pursuit are generally unaffected. These are arguments against a motion processing deficit (Clementz, 1996; Lencer, Trillenberg et al., 2004; Sweeney et al., 1999), at least with regard to processing of retinal velocity information. This shows that despite numerous studies that have investigated visual tracking of continuous motion in schizophrenia, there is not yet a consensus on the cause of this deficit. The use of apparent motion described in the current thesis may assist in uncovering more about the nature and causes of the tracking deficit in schizophrenia.

The potential of apparent motion paradigms in the study of disordered tracking was first pointed out by Slaghuis et al.(2007a), who demonstrated that the tracking of jumping-dot motion resembled disordered tracking in schizophrenia. They also found that the proportion of observers with schizophrenia showing the tracking deficit is increased significantly by using an apparent motion paradigm (Slaghuis et al., 2007a). This thesis has revealed a number of additional applications of these paradigms to the study of visual tracking deficits. First, the current findings show that mechanisms underlying smooth pursuit and saccadic eye movements are different at slow and fast target speeds. Investigating disordered visual tracking as a function of a wide range of target velocities may therefore reveal more about the underlying causes of the visual tracking deficit in schizophrenia. The question remains whether the deficit is present at slow and fast target speeds, with some existing evidence suggesting that they are only present when tracking high velocity targets (20-30 deg/s Clementz & McDowell, 1994; Levin et al., 1988; Thaker et al., 1999). Second, the spatio-temporal conditions resulting in optimal single-mode pursuit gain in observers with schizophrenia and controls in response to both continuous and apparent motion stimuli should be

investigated. This may reveal whether there is a specific smooth-pursuit deficit associated with schizophrenia. For example, Bruno (2005) reported that saccadic activity in observers with schizophrenia, but not in controls, was greatest at slow target speeds (5.0 and 10.0 deg/s). Inspection of the function of single-mode pursuit gain as a function of target velocity may be able to clarify whether this finding is a consequence of observers with schizophrenia having peak pursuit gain at different target velocities for a given target stimulus. Finally, the current findings demonstrated that single-mode pursuit eye movements in normal observers are enhanced by the additional motion signal available in slashed motion and this effect is greater with increasing stimulus duration. If this effect is not found in observers with schizophrenia this may indicate a deficit in the processing of the retinal velocity signal in schizophrenia and a reliance on position signals or other inputs to drive pursuit. In a similar way that these paradigms can be applied to the investigation of the visual tracking deficit in schizophrenia, they could also inform research into other areas of eye movement research.

Summary and conclusions

This thesis describes a series of experiments that demonstrate for the first time that smooth pursuit eye movements in response to both continuous and apparent motion stimuli follow an inverted U-shape pattern as a function of stimulus velocity. The optimal target velocity resulting in the peak of this function depends on the spatio-temporal parameters of the motion stimulus, including stimulus duration and spatial separation. The mechanisms underlying the decline in single-mode pursuit gain are different at target speeds above and below a given optimal pursuit velocity. When

target velocity is slower than the optimal pursuit velocity for a given stimulus, smooth pursuit is not sufficiently engaged, because the combination of spatio-temporal parameters of the continuous or apparent motion stimulus at those target speeds does not allow adequate integration of the signals into an integrated motion signal driving pursuit eye movements. At target speeds above a given optimum velocity smooth pursuit is fully engaged, but eye velocity reaches an upper limit after which eye velocity is slower than target velocity, resulting in the eye lagging behind the target. Furthermore, the current findings demonstrate a very close and dynamic interaction between saccadic and smooth pursuit eye movements. The magnitude of the saccadic contribution to dual-mode tracking increases when single-mode pursuit gain decreases, but the nature of this contribution differs at slow and fast target velocities. A large number of smaller, slower, and briefer saccades are generated to compensate for the low pursuit gain when target speed decreases below optimal pursuit velocity for a given target stimulus, but a small number of saccades of greater amplitude, peak velocity, and duration covers the motion trajectory at fast target speeds. This interplay of saccadic and smooth pursuit eye movements supports more recent models of saccade coordination (Krauzlis, 2005; Orban de Xifry & Lefèvre, 2007), which propose shared underlying processes and neurology, including shared visual processing and target selection for saccadic and smooth pursuit systems (Liston & Krauzlis, 2003, 2005). The results of this thesis also demonstrate that visual tracking of continuous and apparent motion stimuli is generated by the same underlying mechanisms, with similar patterns for single-mode pursuit gain and saccadic variables as a function of target velocity, but with peak performance shifted to faster target speeds in response to apparent motion stimuli. The results are consistent with the idea that continuous and apparent motion stimuli exist on a continuum. This allows motion

signals to be decomposed in a systematic way, providing graded levels of visual motion energy, with slashed motion closer to continuous motion because of the added velocity signal. Finally, the findings of this thesis extended previous evidence for shared inputs for visual motion perception and smooth pursuit eye movements by demonstrating that motion sensitivity and single-mode pursuit gain have very similar inverted U-shape patterns as a function of target velocity in response to both continuous and apparent motion stimuli, suggesting similar spatio-temporal integration of real and apparent motion, consistent with proposals of shared processing beyond area MT (e.g., Stone & Krauzlis, 2003). These findings also have exciting implications and applications to further research of visual tracking in normal observers as well as the study of disordered visual tracking.

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Appendices

Appendix A. Screening questionnaire used in all three experiments.

Please answer the following questions. All your answers are confidential.

1. Your age: _____

2. Do you have any problems with your vision? ☐YES ☐NO

   If yes, please specify _____

3. Do you suffer from any psychiatric illness? ☐YES ☐NO

4. Has any of your close relatives ever been diagnosed with schizophrenia or experienced psychosis?

   ☐YES ☐NO

5. Do you have epilepsy? ☐YES ☐NO

6. Do you have any neurological condition? ☐YES ☐NO

7. Do you suffer from migraines? ☐YES ☐NO

8. Were you ever diagnosed with ADHD or Dyslexia?

   ☐YES ☐NO

9. Are you a regular smoker? ☐YES ☐NO

10. Have you recently used illicit drugs? ☐YES ☐NO